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SPATIAL BEHAVIOR OF FISH AND FISHERMEN: THE USE OF HABITAT SELECTION AND OPTIMAL FORAGING THEORY IN FISHERIES

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Spatial Behavior of Fish and Fishermen:
the use of Habitat Selection and
Optimal foraging Theory
in Fisheries

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Spatial Behavior of Fish and Fishermen :
the Use of Habitat Selection and
Optimal Foraging Theory
in Fisheries

by

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of the requirements for the degree of

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Abstract

SPATIAL BEHAVIOR OF FISH AND FISHERMEN :
THE USE OF HABITAT SELECTION AND OPTIMAL
FORAGING THEORY IN FISHERIES

by PABLO ARENAS

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This dissertation addresses the ecological problem of relaxing some of the homogeneity constraints present in fisheries population dynamics and assessment models. These constraints include the assumption of habitat uniformity and of phenotypically identical individuals, as well as the proportionality of fishing effort and fishing mortality which require a uniform distribution of fish or complete mixing. The subject of study are clupeoid fisheries, with special emphasis in the northern anchovy (*Engraulis mordax*) fishery of Baja California Norte, México and Southern California in the U.S.

The general objective of this work is to examine the concept of a fish population as structured (individuals are not identical) and fluid (due to biotic and abiotic factors local density changes over space and time), its ecological implications and interaction with local perturbations (e.g. fishery harvesting rates).

The problems of fish behavior, or determining to what extent a population displays spatial flexibility are explored by describing the heterogeneity and dynamics of clupeoid populations as they relate to movement. The expansion and contraction of range, and the ecological ideas of density dependent habitat selection and the ideal free distribution are examined in this context.

The question of fish population structure and intraspecific variability is explored by describing the clinal variation in growth and mortality rates of clupeoid fish populations.

The issues related to the spatial heterogeneity of the anchovy fishery and fish behavior are studied by describing temporal and spatial variation in aerial effort, sightings and catch rates in both Mexican and U.S. waters. The local spatial scope of the fishery, in particular the nature of concentration rings of effort and harvest rates around the main fishing ports are also examined. An analysis of the mean distance fishermen are willing to travel for harvesting anchovy, as influenced by

biological and economic factors, is also performed.

To analyze some implications of these heterogeneity issues in fisheries assessment and management, the ecological theory of foraging is adapted to a fishery system. The particular case of central place foraging is used as an analogy to the fishermen-fish interaction in a small, centrally located fishery in which fishermen must return to the fishing port after a relatively short fishing trip. The basic central place foraging model is adapted to account for particular constraints of the anchovy fishery in México and the U.S. These include a limited maximum total fishing time available, the limit imposed on landings by canneries, the effects of area closures and the use of scouting airplanes. The resulting model is particularly useful for the assessment of effects of area closures in small pelagic and demersal fisheries.

In this work it is demonstrated that the alternative view of considering fish populations as spatially flexible and made up of distinct individuals can be very useful to the understanding of fish population dynamics and could also provide insight into the ecological problem of spatially fluid populations and population regulation. Similarly, the alternative view of considering fleet dynamics and in particular movement patterns can be very useful to the understanding of fishing systems, and could also provide valuable insight into fisheries management problems.

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DEDICATION

This dissertation is dedicated to:

My parents Esperanza and Gonzalo, who have helped me throughout my life and career by giving me the freedom of choice.

My brothers and sisters: Beatriz, Virgilio and Eugenia, Eva and Luis, Pedro and Martha, Gonzalo and Pat, and María, who have always provided love, friendship and have set examples to follow.

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INTRODUCTION

Most theoretical models of population regulation consider the population as a collection of phenotypically identical individuals inhabiting spatially homogeneous habitats. Only during the last decade a few of these models have incorporated temporally and spatially varying environments. A general review can be found in Stenseth (1980).

The ecological effects of habitat heterogeneity and its relation to population dynamics are, however, topics that yet have to be explored. Disregarding the theory of Island Biogeography (MacArthur and Wilson, 1967), which explores the most extreme case of habitat heterogeneity, the topic is only lightly explained even in general works such as Rougharden's (1979). On the other hand, spatial heterogeneity and the patchiness that it is usually assumed to produce, are explicitly considered in models of habitat selection and optimal foraging theory (Rosenzweig 1974, 1979a, 1981, Charnov 1976). Patchiness has also been explained by social behavior, particularly among vertebrates (Wilson, 1979).

These studies of local behavior, however, do not consider the large scale necessary to understand distribution over the entire range of the population (but see Brown 1984), so population dynamics and regulatory problems are seldom considered within this context. The approach of Rosenzweig 1979b, Pimm and Rosenzweig 1981 and MacCall 1984 is an exception as they treat habitat selection and population dynamics simultaneously.

Relaxing the assumption of phenotypically identical individuals has proven to be a complicated topic. The traditional models usually stress the importance of the number of individuals and total biomass and assume that the only differences among individuals that are of ecological importance are those related to age and sex. Theoretical ecology usually accepts age-dependent and hereditary differences among individuals in fecundity and survival, but differences of other origin are neglected and population members are considered in theoretical models as molecules indistinguishable from one another (Lomnicki, 1978, 1980).

Yet, it is a well known fact that intraspecific variation in growth and survival occurs, and should be taken into account to explain population regulation. This topic has been studied in some detail by plant ecologists (see Sarukhán *et al* 1984), but has received almost no attention from animal ecology. An exception is Lomnicki's

model (1978,1980) which attempts to explain population regulation considering individual variation (not necessarily hereditary), in the form of differential resource intake in a heterogeneous environment.

Another important complication arises if we consider explicitly individual movement, because according to these homogeneity-oriented models, population change can only be assigned to reproduction and mortality, the key factors in population regulation being associated with the causes and time of death and reproduction, but not with the place of death nor to its distance and direction from the place of birth. Thus, relaxing the assumption of homogeneous habitat and identical individuals allows us to consider the movement of individuals as an important component of population regulation. However, how habitat heterogeneity and the potential for movement can together influence population dynamics is a topic that had not received attention until a few years ago (Hassel 1980), despite important papers during the 1950's (Hutchinson 1951, Huffaker 1958) and the long-recognized importance of movement upon genetics and demography (Lidicker and Caldwell 1982). The importance of individual movement (e.g. dispersal and migration) has been at the center of the group selection controversy, because the movement of some individuals into hostile or suboptimal areas, being of selective disadvantage for the moving individuals (MacArthur 1972), cannot evolve by individual selection. The evolution of individual movement and other behavioral mechanisms of population regulation has been therefore explained by group selection (VanValen 1970, Gilpin 1975). However, Lomnicki (1978,1980) has shown that movement can regulate population, evolving under individual selection if individual differences in resource intake amongst individuals in a heterogeneous habitat are taken into account (see also MacCall 1984). In this way the consideration of movement transforms the traditional time-based unidimensional model of population dynamics into a new population concept on a space-time continuum. This view of population is a truly dynamic one, with individuals in constant motion, and local populations changing in space and time. Taylor and Taylor (1977,1980) and Taylor *et al* (1979) have proposed a model in which populations are spatially fluid in some characteristic over both ecological and evolutionary time scales. They consider that movement is the ultimate consequence of all behavior and that it affects population regulation and redistribution if an individual is born in a different place from that of its parents.

This dynamic anatomy of populations made up of individuals in a state of flux in real space as well as in real time, that is, considering populations as existing in three dimensions (latitude and longitude through time) allows to visualize its structure to be reticulated (e.g. the stern stele conceptual model of Taylor and Taylor 1977, see Figure 1) in which local density changes constantly through time and space. This structure adapts populations through habitat selection to their ever changing environment and so provides both dynamic stability and resistance to evolutionary change. The authors conclude that the study of spatial relationships could account for the paradox of limiting resources as the key to classical population theory, when resources are very frequently only locally limiting in nature.

Relaxing these homogeneity assumptions has not been considered in detail in fisheries literature, since most fisheries models have been adapted from the field of ecology and mathematically it is more difficult to deal with the added complication of fishing mortality, which can be in itself both temporarily and spatially heterogeneous. The models most used for management fall into two categories: the dynamic pool models (e.g. Ricker 1975, Beverton and Holt 1957) and surplus production models derived from the logistic equation (e.g. Schaefer 1957, Pella and Tomlinson 1969). Both approaches deal with a stock (in fisheries a stock is loosely equated to population) considered as a closed, (e.g. no interaction with the exterior) self sustaining group of individuals forming a unit within which fishing mortality is proportional to fishing effort (Cushing 1981). This definition has received frequent criticism (for a review see Gauldie 1985) but it is widely used due to its practical simplicity and intuitive appeal. However, the proportionality of fishing effort and fishing mortality requires a uniform distribution of fish and a random distribution of effort over the fishing area and requires also that each unit of effort be considered independent. Unfortunately, because a stock is often contagiously distributed, an entire population is not equally vulnerable to fishing effort. Moreover, because fishermen make rational decisions in selecting fishing locations, effort is itself neither random nor independent.

In order to reconcile this spatial heterogeneity of both fish and fishermen with the theoretical homogeneity requirements, active mixing (e.g. individual intrastock movement) is usually assumed to spread local effects of fishing effort uniformly across the unit stock, so that local areas which have been depleted are replenished by this individual intrapopulation movement (Caddy 1975). In this respect the view

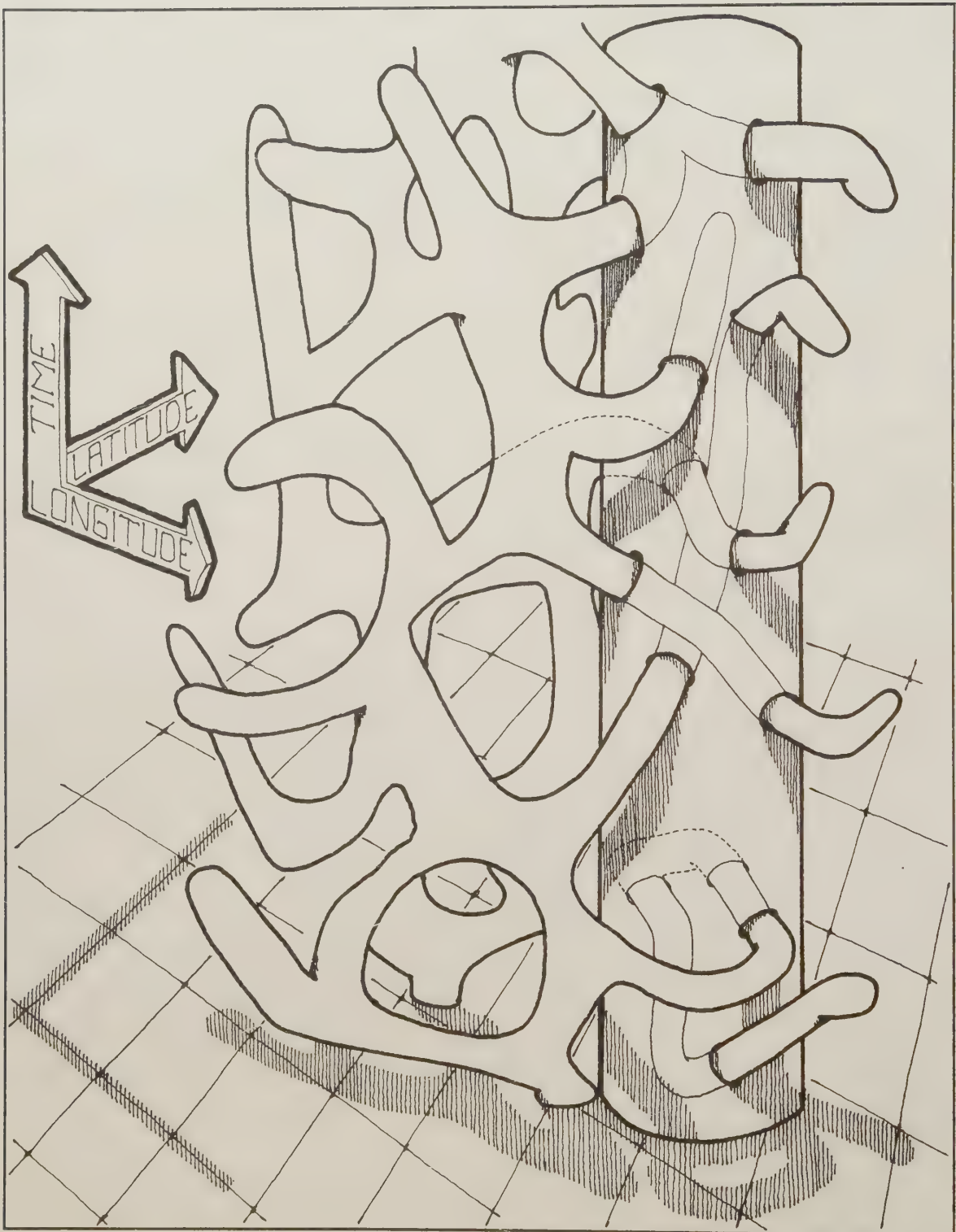


Figure 1. The Stern Stele Model. The stele represents the space-time reticulum created by the distribution of an arbitrary density level trough time. The cylinder represents the maximum area of influence of a local perturbation. Based on Taylor and Taylor (1977).

of a unit stock discussed above has however, some limitations:

One set of problems is related to the assumption of complete mixing (uniform distribution of fish) and, since a stock definition limited so rigorously, although it serves sometimes for a well defined administrative role but has almost no biological meaning, the consequence is that few fish populations meet the requirements to be considered a stock; therefore the application of management measures based on homogeneous models has to be made with caution. The problems arise mainly because either the animals move in and out of the stock “limits” or else internal mixing is insufficient, producing clumped or non homogeneous distributions. The result is that there is no generally accepted, formal ecological theory of stocks that accounts for their distribution, range of population size, and the associated life-history parameters (Iles and Sinclair 1982).

The other set of limitations arises as a result of the non random distribution of fishing effort and the non independence of fishing units. Little attention has been paid to the consequences of violating these assumptions, despite the fact that they are implicit in most fisheries models. In particular, effort allocation, harvest efficiency and the movement patterns of a fishing boat (e.g. when, where and how to fish) are aspects of fleet dynamics that have received almost no attention (Hilborn 1985a), despite the generally recognized fact that the understanding of the relationship between fish abundance and catch per effort requires a knowledge of the behavior of fishermen and its consequences upon the fishing process as well as the knowledge of the behavior of fish as it affects the spatial distribution of the resource.

In this dissertation I address the ecological problem of relaxing some of these homogeneity constraints, using a fishery system as example. First I describe the heterogeneity of a fish population and some of its dynamics as they relate to movement (expansion-contraction of range) and intraspecific variability (clinal variation in growth and mortality rates). Subsequently I describe patterns of movement dynamics of the fleet and discuss some ecological thinking (in particular foraging models) that can be used to understand these patterns, and eventually could help in the management of fish resources. Therefore, the general problem that this study addresses is the result of the interaction between a local perturbation (e.g. the consequences of a fishing fleet with limited range) and the concept of spatially fluid populations (e.g. the effects of expansion-contraction, clinal variation and incomplete mixing). One of the practical aspects of this dissertation is that the

models can be used to evaluate the consequences of different management strategies for fishery systems which exhibit this type of behavior.

Clupeoid fisheries (e.g. sardine and anchovy) are a useful example for such a study because they are an economically important world resource and have been intensively studied. Also, they show spatial flexibility in the form of expansion and contraction of spawning and breeding range with changes in density (Murphy 1977, MacCall 1984) and preliminary studies have showed that at least some clupeoid populations are structured by age and size, with a relatively low degree of mixing among "subunits" (Felin 1954, Mathisen 1979, Parrish *et al* 1985). In addition, due to the nature of the fish resource as well as to the characteristics of the fishing fleet and the processing plants, the effort in many fisheries is usually spatially constrained to the coastal area and its range is very restricted relative to that of the population.

The northern anchovy (*Engraulis mordax*) fishery of southern California (United States) and northern Baja California (México) provides an excellent opportunity to study these problems, because it exhibits the characteristics described above, and because there is a large amount of data related to the fishery and its environment collected by monitoring programs. For example, the California Cooperative Oceanic Fisheries Investigations (CalCOFI) Program has monitored abundance and distribution of northern anchovy larvae and oceanographic variables off California regularly since 1951. The fishery itself has been monitored regularly by State and Federal agencies both in México and in the USA.

The purpose of the study is then to examine the interaction between a local fishery and a spatially fluid, structured population. Therefore the general objective is to study the concept of a population that is structured (individuals are not alike) and fluid (local density changes over space and time) population, its implications and their interaction with local perturbations (fishery harvesting rates). The problem of study might be further clarified by asking a number of general questions :

- In what ways and to what extent does the population display structure and spatial flexibility ?
- What kind of patterns are typical of a "local" fishery ?
- What are the implications for assessment and management ?

The objective of each chapter is directly related to the general questions stated above. The body of the Dissertation is presented in Chapters I through III and the main components of each chapter are synthesized and discussed in Chapter IV titled "Summary and Discussion".

Chapter I titled "Heterogeneity of Clupeoid Populations" concerns itself with the behavior of fish, both in space and time. The expansion and contraction of spawning and feeding grounds phenomenon is reviewed as part of the flexibility exhibited by the population, and the clinal variation in growth and mortality rates is discussed as an example of population structure.

In the next two chapters, I consider some aspects of the behavior of fishermen, both empirically and theoretically :

Chapter II titled "Heterogeneity of the Northern Anchovy Fishery" describes the temporal and spatial variations in aerial effort, sightings and catch rates in both Mexican and USA waters. The very limited spatial scope of the fishery is also described in this chapter, in particular the nature of the concentration rings of effort and harvest around the main fishing ports, and the mean distance fishermen are willing to travel for harvesting, as influenced by biological and economic factors.

Chapter III titled "Fisheries and Optimal Foraging Theory" explores the possibility of application of ecological models of foraging, in particular the Central Place Foraging Theory as an analogy to the Fishermen-Fish interaction, and discusses some of the derived implications, as well as limitations of the theory.

In Chapter IV titled "Summary and Discussion" I synthesize the principal components of the preceding chapters and I discuss some of the most important findings and opportunities for research.

This alternative view of considering fish populations as spatially flexible and made up of distinct individuals can be very useful to the understanding of fish population dynamics and could also provide valuable insight into the general

ecological problem of spatially fluid populations and population regulation. Similarly, the alternative view of considering fleet dynamics and in particular movement patterns can be very useful to the understanding of fishing systems, and could also provide valuable insight into some management problems.

CHAPTER I HETEROGENEITY OF CLUPEOID POPULATIONS

I INTRODUCTION

The study of distribution and abundance is one of the central problems in ecology and biogeography, and the main issue of population ecology, but although it has been long recognized that abundance and distribution are intimately related, there is no systematic theory that accounts for the patterns in the changes in spatial distribution and local population density over the entire temporal and spatial range of a population (Brown, 1984). The local scale, i.e. the small habitat patches where most ecological studies are carried out, has been generally well studied and is the traditional field of many studies in population and community ecology, producing important contributions (see the general review of Krebs, 1978). On the other hand, distribution over a large geographical scale has usually been the special province of Biogeography and has resulted in few empirical population studies. Some theoretical aspects have been explored by MacArthur and his colleagues (e.g. MacArthur and Wilson 1967).

Many of the problems in working over a large geographical scale are a consequence of the lack of clear definitions of population characteristics involved in the changes in spatial distribution with changes in total abundance. For example **range** is a characteristic which depends highly on the sampling scale used, and which is ultimately discrete if a fine enough scale is utilized because every individual is either present or absent. Thus, a large measuring scale may produce the impression of a very uniform distribution, but the same population will appear patchily distributed if a small measuring scale is used. This problem is particularly noticeable where two or more species are mixed, usually at the distribution boundaries (see Rapaport, 1982 for a discussion of some of these "indefinitudes"). In many studies some of these quantities have only been measured subjectively and this situation makes it difficult to adequately evaluate these population attributes. This is a particularly difficult problem when assessing local density changes and spatial distribution in a specific location with some regularity in time. This is the reason why there are only a few time series on population spatial changes that cover a geographically large area.

In what follows I shall adhere to Brown's (1984) usage of some terms related to the density of individuals within a local area, and to the extent of the distribution of individuals in space. The term **abundance** refers to local population density (in number of individuals per unit area) and the term **rare** and **common** (or **abundant**) describe extremes of density. The terms **distribution** or **range** refer to the extent of spatial distribution and the terms **restricted** (or **local**) and **widespread** describe the extremes.

This chapter addresses the population heterogeneity problem in clupeoid fish populations by means of describing changes in spatial distribution as they relate to changes in abundance over large geographical areas. This characteristic is referred to as **spatial flexibility** of a fish population. The problem of ecotypic or clinal variation in population features such as natural mortality and growth rates is also considered, and is referred to as **spatial structure** of a fish population. Additionally, the problem of **mixing** will also be discussed, as the fish populations under consideration exhibit enough heterogeneity as to warrant the consideration of the problem of dispersal and migration among different segments of the population. Finally, some general considerations related to exploitation will be examined, with particular attention to the case of a spatially restricted fishing fleet harvesting a fish population which exhibits both flexibility and structure.

II SPATIAL FLEXIBILITY

EXPANSION AND CONTRACTION

One of the ecological characteristics of spatial flexibility more easily distinguished over time is the expansion and contraction of the area occupied by the population. This issue has been largely studied from the standpoint of evolutionary biology, in particular in relation to the evolution of a taxonomic unit and the physical barriers the group encounters during the process of dispersion and colonization of new environments. However, the problem posed by changes in population density in the expansion and contraction of range over a large geographic area has not received attention from ecology and is a relatively new research

topic. Some of the typically postulated processes of taxon expansion and contraction are illustrated in the diagrams in Figure 2 (After Rapaport 1982, modified from Darlington 1957). Figure 2a shows the basic expansion and contraction concept. The population range is increasing and decreasing, but the center of the population distribution is spatially fixed. Figure 2b illustrates the expansion and contraction of range with movement, resulting in a change in the center of distribution. Figure 2c is the same process but with a preferential direction or a range drift in which the entire population is moving. Figure 2d illustrates a cycle of expansion and contraction and final disjunction, ending in the formation of two distinct subunits or cells. Diagram 2e represents the crossing of a barrier, with the subsequent expansion and contraction in a previously unexploited area.

Rapaport (1982) considers that these processes and the diagrammatical models illustrated in Figure 2 are also valid in microgeographical scales, and they can easily be adapted as well for the study of changes in spatial distribution of a single population undergoing changes in abundance.

Despite early empirical observation regarding the ecological importance of the distribution and abundance of individuals, some of these patterns of expansion and contraction with changes in density have been considered as an integral part of the population ecology of several species groups only recently (see MacCall 1984 for a summary). Some of the species showing expansion and contraction of range with changes in population size are indicated in Table 1.

As is shown in Table 1, this process has also been observed among fish, in particular in species where adult individuals exhibit a strong tendency to form schools, such as members of the sardine-like clupeoid family (i.e. sardine, herring, anchovy). These species form the basis of large fishing industries in many countries, accounting for roughly a third of all the fish caught worldwide (Murphy, 1977). Many populations of these species exhibit expansion and contraction of range, in particular they show a marked reduction and increase of feeding and spawning areas with changes in overall abundance.

Fishing activity affects abundance in these populations because exploitation is a major component of mortality and this, in turn, has an effect on the expansion and contraction patterns which, closing the cycle, have a feedback effect on fishing. It is very likely that the interplay of these factors in combination with environmental changes is what makes these species so prone to overexploitation and economic extinction.

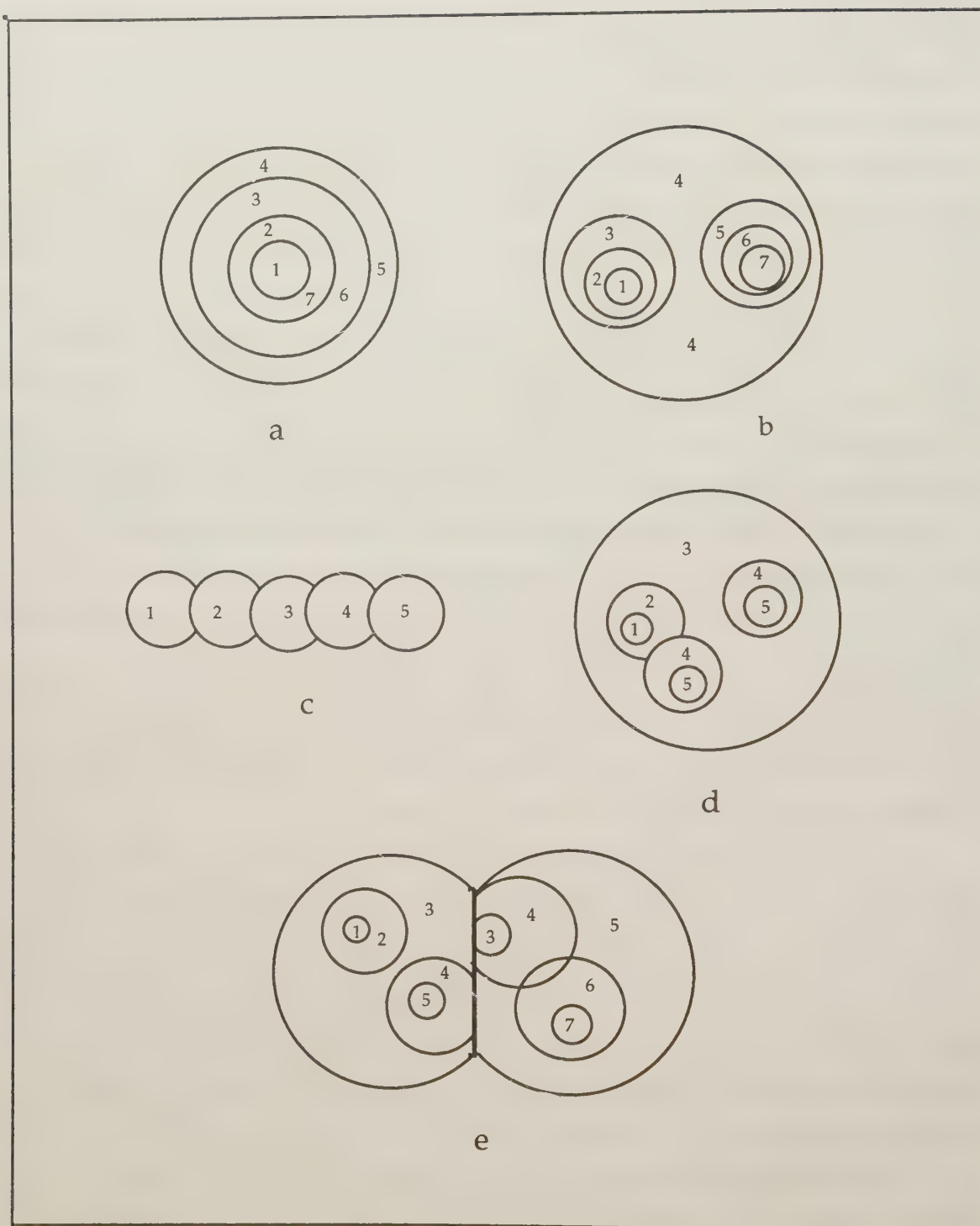


Figure 2. Typical processes of expansion and contraction of ranges of population distribution. a) Expansion and contraction in the same place. b) Expansion and contraction with change of center. c) The whole population moving. d) Expansion, contraction and final disjunction. e) Expansion, contraction and colonization of a new habitat. Numbers denote time steps. Modified from Darlington (1957).

Table 1. Examples of species showing expansion and contraction of range. Modified from MacCall (1984).

Fish	northern anchovy	Kramer and Ahlstrom (1968)
	Japanese sardine	Kondo (1980)
	Peruvian anchoveta	This work
	North Sea herring	ICES (1970)
	South African pilchard	Crawford <i>et al</i> (1980)
	Atlantic Menhaden	Schaff and Hunstman (1972)
	minnows	Fraser and Sise (1980)
Birds	canary	Mayr (1926)
	ducks, gulls	Svardson (1949)
	titmouse	Kluiver and Tirbengen (1954)
	chaffinch	Glas (1960)
	blackbirds	Lenington (1980)
Insects	aphids	Whitham (1980)
	bees	Thomson (1978)
Reptiles	<i>Anolis</i> lizards	Schoener and Schoener (1980)
Small Mammals	lemming	Pitelka (1973)
	snowshoe hare	Wolff (1980)
	gerbils	Rosenzweig and Abramsky (1985)
Large Mammals	baleen whales	Allen (1972)
	elephant seal	Bodkin <i>et al</i> (1985)
	man	Gordon (1954)

Habitat Selection

One of the main factors determining the ultimate spatial distribution of populations is the behavior of individuals when selecting a place to spawn or to live. This is the reason why behavioral ecology and in particular the Theory of Habitat Selection provides a basic framework for the study of this subject. Habitat Selection refers to the choice of a type of place in which to live: Why do some individuals prefer some particular place and avoid others? The answer is that they behave this way because this is a process modulated by Natural Selection to favor those individuals that choose the "right" habitat, meaning by this those places in which most progeny can be raised. Those individuals who choose poor, marginal habitats cannot reproduce as successfully on the average and are therefore selected against. This process of habitat selection can be regulated both behaviorally and genetically. Since a habitat imposes a particular selection regime which modifies the phenotype of individuals, the selection of a particular place has important consequences for the population.

Despite the fact that this is an important problem in ecology, it remains one of the most poorly studied and understood. Partridge (1979) offers a general review of the subject in which it is shown that among the topics that have just begun to be explored are the way in which habitat preferences interact with other factors to produce distributions in nature; the development of habitat preferences and their adaptive significance, and the cues used by individuals to assess how good a particular habitat is. Part of the problem in investigating habitat selection is due to the large temporal and spatial scales necessary to assess the ecological and evolutionary importance of all the choices an individual makes when selecting a place to live.

Density Dependent Habitat Selection

The problem of how habitat preferences interact with abundance to produce spatial distributions is of particular importance to the expansion and contraction of feeding and spawning ranges. This subject has been examined theoretically (e.g. Morisita 1971, Fretwell 1972, Rosenzweig 1981, MacCall 1984); it has been observed empirically both in the laboratory (Morisita 1952, Kosaka 1956, Holmes 1961) and in

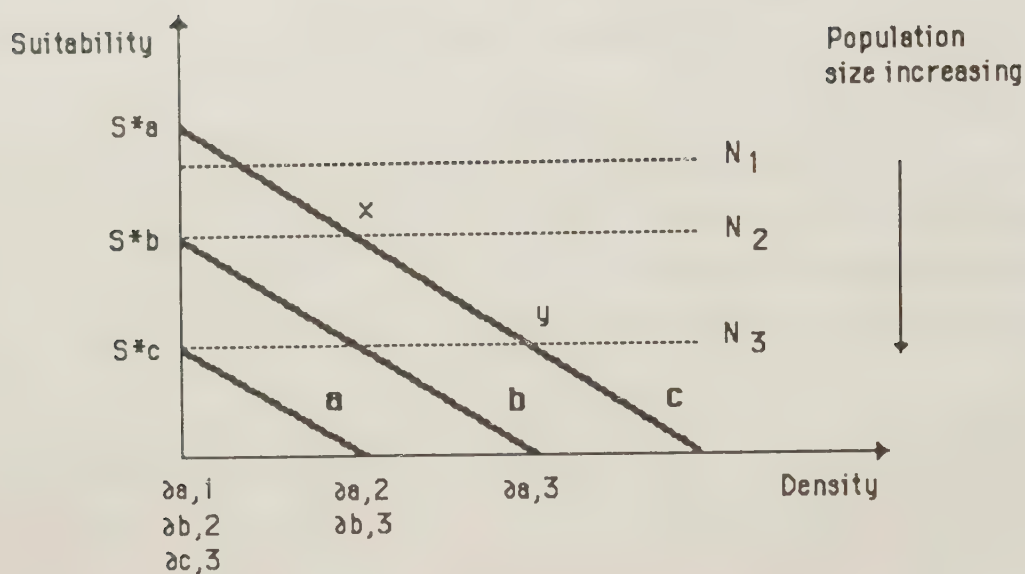
the field (MacCall 1984, Pimm et al 1985).

The theoretical aspect of Density Dependent Habitat Selection (DDHS) has received different treatments in ecology, mainly by ornithologists (see MacCall 1984 for a general review of its historical development). In those empirical studies in which abundance has varied markedly it has been noticed that the organisms tend to occupy progressively more marginal habitat with increasing abundance, a process which produces the above discussed expansion of range (see Figure 2 and Table 1). With decreasing abundance the process acts in the opposite direction, and individuals occupy preferentially the central, presumably better habitat.

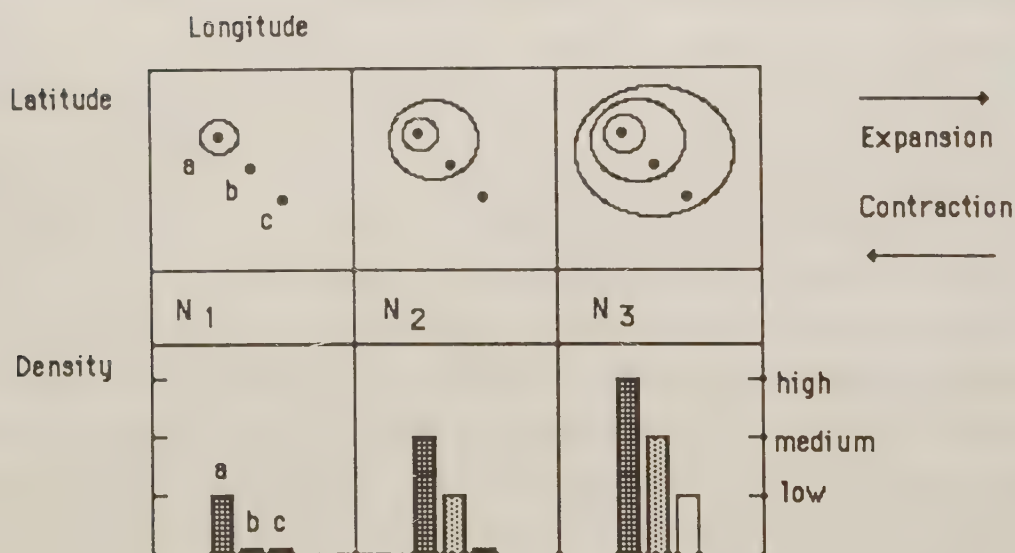
Ideal Free Distribution

One of the most interesting treatments of Density Dependent Habitat Selection is the Fretwell-Lucas theory (Fretwell and Lucas 1970, Fretwell 1972, Whitham 1981, Rosenzweig 1981, MacCall 1984) which proposes the existence of many discrete habitats that can be ordered in terms of their relative "quality" or suitability.

The basic assumption of the theory is that Natural Selection will favor those individuals who select the best habitat (e.g. the most suitable in terms of its probability of leaving more progeny in the next generation) among the available areas. In the absence of territoriality, the ultimate result of this selective behavior is what Fretwell and Lucas (1970) called the Ideal Free Distribution (IFD). The principle is as follows: In Figure 3, three habitats are shown: **a**, with high suitability; **b**, with medium suitability and **c**, with low suitability. In all habitats the rate of reduction in suitability (S) with increasing density is linear, and equal for all places. There are also three population levels represented by horizontal lines intersecting habitat suitability lines. Each habitat has a basic, maximum suitability at zero density (S_a^* , S_b^* and S_c^*). The Ideal Free Distribution arises because the individuals arriving first will chose habitat **a**, which offers the highest suitability S_a . However, the quality of the habitat decreases due to density dependent effects until point **x**, where $S_a = S_b^*$. Habitat quality in **a** is now equal to the basic suitability in **b**. At this point, new arriving individuals have two choices offering the same suitability, habitats **a** and **b**. The lower suitability in this formerly marginal habitat is compensated by an increase in area per individual (e.g. lower density). Some animals will go to **a**, some will go to **b**, and both S_a and S_b will decrease. However, density in both habitats should increase in such a way that $S_a = S_b$. This process continues until point **y**, where $S_a = S_b = S_c^*$ and the three habitats offer at this abundance level the same



a



b

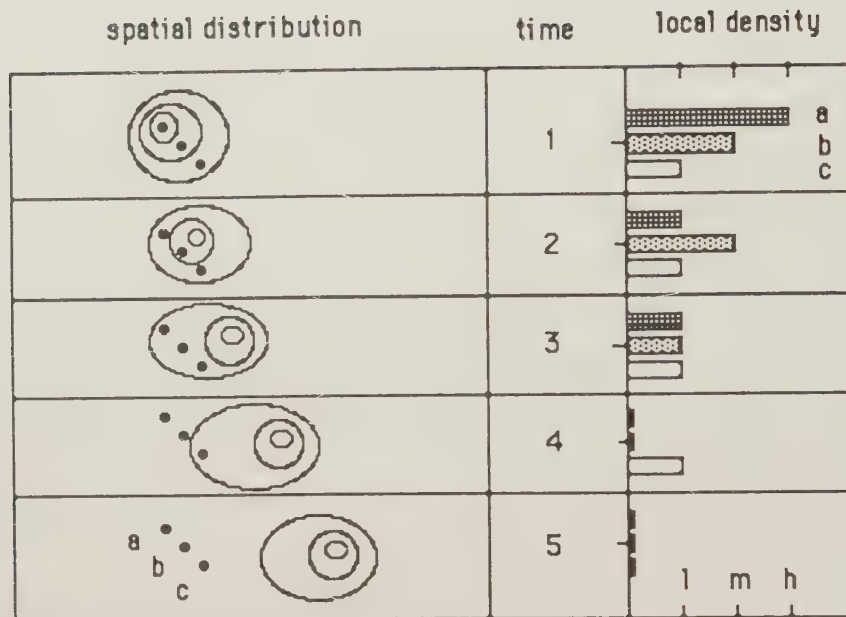
Figure 3. The effect of population density on habitat selection and the generation of cycles of expansion and contraction of range. a) Local suitability and density. b) Spatial distribution and local density. ∂_{ij} = density in habitat i at population size j . N_1, N_2, N_3 are population sizes. a, b, c are habitats with varying suitability. See text for an explanation of the figures. Diagram a based on Fretwell, 1972.

expected success to newly arriving individuals. This mechanism will generate an expansion cycle, as individuals settle in a at first, then in a and b, and finally in all three habitats, a, b, c. At the highest density the population will occupy the largest area that can offer adequate resources, and a process of expansion of range will have taken place. Habitats attract and support population densities in proportion to their resource opportunities. The opposite mechanism works when as the population total abundance decreases. A low proportion of the marginal areas is occupied because the newcomers prefer to settle in the central areas where the average per capita suitability is higher. The marginal habitat quality is no longer comparable to the central areas due to the decreased density. As this process continues, the population will contract its range leaving more areas unoccupied in the periphery. Thus, alternative cycles of expansion and contraction of ranges can be brought about by this density dependent mechanism of selective behavior.

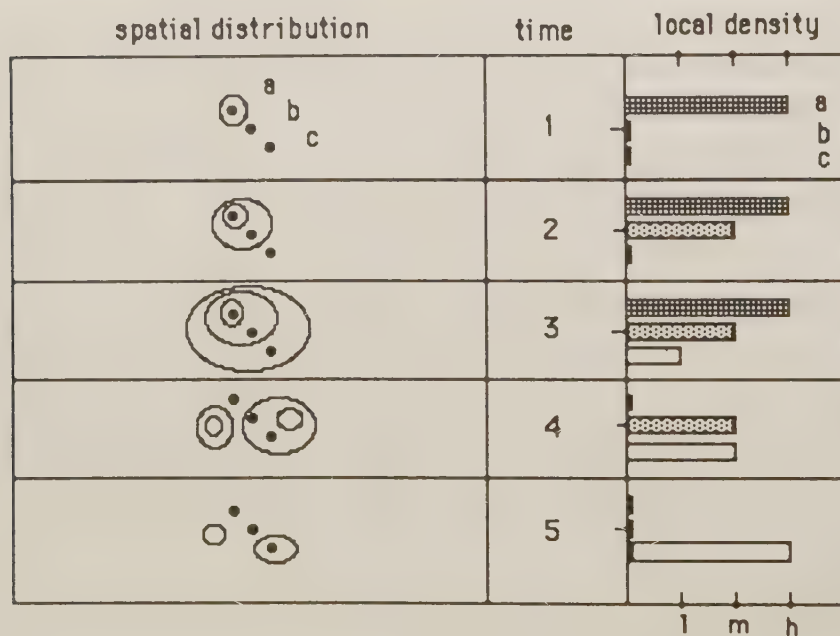
Notice that when population increases density also increases for a particular area ($\partial a,1 < \partial a,2 < \partial a,3$). Also, the model predicts that local density will always be highest in the center of the range, decreasing toward the periphery ($\partial a,3 > \partial b,3 > \partial c,3$). This has been shown to be a general property of populations (Brown 1984) for a wide range of animal and plant groups. Notice also that the center of the population is not necessarily fixed in space (see diagrams in Figure 2), as its location depends not only on density (which produces intraspecific competition), but also on environmental conditions (e.g. El Niño's high temperatures may make many fish species shift the optimal spawning area center). In this case, local density changes at spatially fixed points will show high variability, making it extremely difficult to estimate population characteristics from spatially fixed samples (Figure 4). Also, interspecific competition increases with the area occupied, and it is presumably higher in the periphery of the range (in fact, this is one of the reasons why the peripheral habitat may be considered marginal). However, both the center of the range and its boundaries may be more related to abiotic than to biotic interactions.

The Ideal Free Distribution theory relies upon several assumptions to explain this density dependent selective behavior :

- 1) Suitability is always a decreasing function of density; there is always a lowering effect on suitability of an increase in population density in a particular habitat. Under certain circumstances this may not be true, because suitability can



a



b

Figure 4. Changes in local density at spatially fixed sites. a) Moving center b) Expansion, contraction and final fragmentation. The small circle represents the area of highest density; the large circle is the area of lowest density; a, b, c are spatially fixed points; levels of local density l = low, m = medium, h = high.

actually increase with increased density, particularly at low densities (Allee's Principle; Allee et al, 1949). Some of the advantages that may contribute to make a particular habitat more attractive are the increased probability of finding food and mates, and the decreased probability of predation. If Allee's principle is operating, the marginal habitat may actually increase its relative value after a few individuals settle in, with the result that a small increase in population size may have a large effect on distribution (Fretwell 1972).

2) The distribution is termed "ideal" because every individual has the capability of choosing the best available habitat. Every individual has a perfect knowledge of the situation and can assess changes in suitability instantaneously. As Fretwell (1972) points out, this seemingly unrealistic assumption is not unreasonable if the same selective pressure has acted for a long time, favoring those individuals that exhibit the ideal behavior. Nevertheless, an individual usually does not have perfect information, so its choices are limited to a restricted set of all the available places. This "imperfect" behavior may have a complex effect on the distribution.

3) Last, it is also assumed that there is no interference to new settlers from prior occupants, meaning that each individual is "free" to enter any habitat, and all individuals within a habitat have identical expected realized suitability. The most obvious violation to this assumption is territorial behavior, whose effect produces a different class of distribution, termed "Ideal Despotism" by Fretwell and Lucas (1970). In this case, those individuals who already occupy a particular habitat have, on the average, better success rates than the newcomers. The violation of this assumption may not be that much of a problem for free swimming, pelagic species among which no territorial behavior is found. However, the assumption of identical expected success requires also that all individuals be alike, and this will only hold if we restrict our attention (Fretwell 1972) to habitats as widely distributed as species or to the local population.

Together, these assumptions imply that there is not a better place for an individual to live or reproduce than the one it has chosen (principle of "equal opportunity" of MacArthur 1965; see also MacCall 1984). Therefore the theory implies that the per capita success or realized suitability is identical in all habitats for a particular population size. From the standpoint of spatial distribution, the ultimate

result of these processes is an expansion and contraction of range with changes in density.

MacCall (1984), modified the Density Dependent Habitat Selection Theory considering the habitat as a continuous "topography". This approach allows to visualize the population as living in a "basin" of topographical suitabilities. If suitability is increasing downward (Figure 5), the population will tend to fill the basin behaving as a liquid. This analogy of population and liquid is useful enough to allow the consideration of many aspects of population dynamics, including the phenomenon of expansion and contraction with changes in density, as these can be depicted by the volume (population abundance) of the liquid and the contours (range of population) of the "lake" (habitat) for different volumes (population levels). This approach is based on the extension (using simple logistic growth of local populations) of Fretwell's (1972) model of discrete habitats to the continuous case of habitat distribution over a large geographical area. Local population growth rates are then functions of local basic habitat suitability and of population density. These growth rates are constrained by the Ideal Free Distribution.

The spatial distribution is maintained by the individual movement of animals responding to gradients in realized habitat suitability, and MacCall (1984) modeled this behavior using the diffusion equation. This equation was developed to explain the molecular dynamics of advection and diffusion, but its use has been extended to the field of Biology (see review by Okubo 1980). By combining the logistic and the diffusion-advection equations, and examining equilibrium properties, the author demonstrated that there is a net flow of individuals from the center of the distribution to the periphery. He postulates also that if the "biological viscosity" (movement of individuals within the population) is low, that is, if the homogeneity assumption holds, then mixing among individuals is complete and harvests have an equivalent effect wherever they are taken. On the other hand, when the population does not mix well (the high biological viscosity case), harvesting has a persistent effect on local abundance. In the high viscosity situation, population losses due to harvest are replaced only by in situ growth, whereas they are replaced by both in situ growth and immigration in the low biological viscosity case.

The consideration of a continuous habitat topography removes one of the major

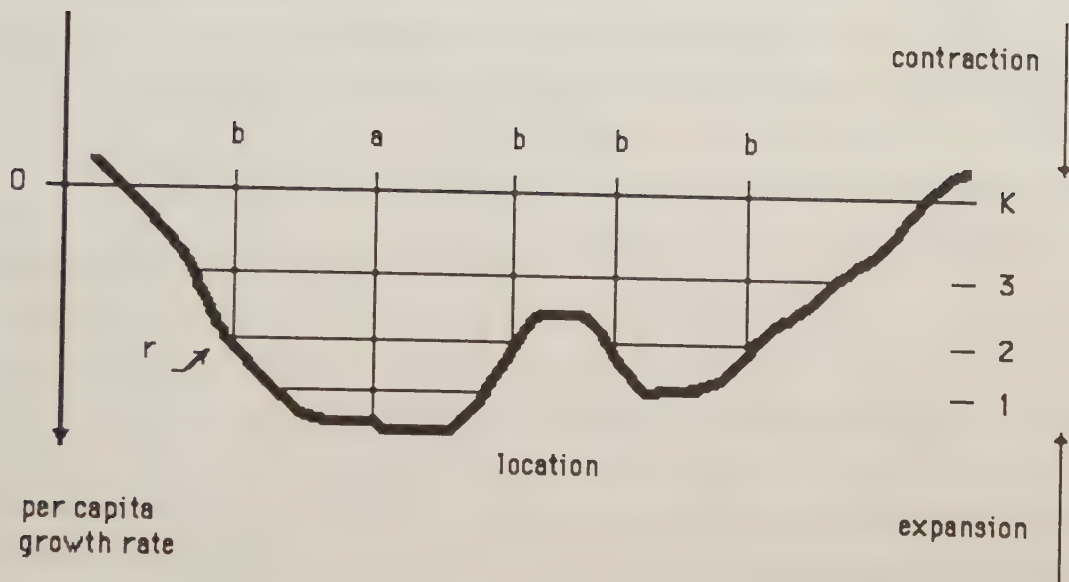


Figure 5. Transect through a continuous geographic fitness topography. 1,2,3, are total population sizes; k represents the carrying capacity; a and b are habitats with varying suitability; r is per capita growth rate. The population will expand from size 1 to 3, due to the Ideal Free Distribution. Based on MacCall (1984).

problems of the discrete habitat theory, because individuals do not need to be aware of the whole range of habitat suitabilities (assumption 2 above), but they need only to respond to local suitability gradients. The population response will be similar to the one predicted by the discrete habitat approach, but the assumption of ideal individuals (e.g. perfect knowledge) has been relaxed.

One of the problems in understanding spatial distributions has been the difficulty in defining habitat suitability and the complications inherent in assessing reproductive success in different habitats. The Ideal Free Distribution as we saw above predicts that suitability (e.g. reproductive success) should be equal in all the occupied habitats, but the imperfect nature of interactions among individuals may produce a spatial distribution in which the "better" adapted individuals tend to selectively choose the central areas, and those that are "less" adapted would tend to accumulate in the periphery, in marginal areas (see assumption 2 above).

MacCall (1984) has proposed to measure realized habitat suitability as instantaneous per capita growth rate (see Figure 5). This quantity provides a convenient analogy to reproductive value, which is a function of habitat, age, and other characteristics. The problem of optimality remains unsolved, but as many authors have shown (Roughgarden 1974, Fretwell 1972), the clues or stimuli influencing the choice of habitat may not be more than correlated with habitat quality: individuals assess optimality according only to the stimuli offered to them. This evolutionary iterative process will only tend to optimality without ever achieving that theoretical state.

Recently, Rosenzweig and Abramsky (1985) have proposed a method for measuring density dependent habitat selection using simple census data. The measure is based on Simpson's index of species diversity, which is widely used in population biology. This method allows to study how selectivity changes with density using multiple linear regression on a transform of Simpson's index. Several hypothesis can be tested with this technique including: random selectivity, constant selectivity (no density dependence), no selectivity, selectivity at low density approaching an ideal free distribution at high density, and hyperdispersion (social and territorial behavior).

EXAMPLES OF DENSITY DEPENDENT HABITAT SELECTION IN PELAGIC FISH

The purpose of this section is to review evidence regarding density dependent habitat selection in the form of expansion and contraction of feeding and spawning ranges for the northern anchovy (*Engraulis mordax*) and other commercially important clupeoids. It is necessary to note that these species are obligated schoolers. This characteristic probably determines the extent to which clupeoid populations conform to the theoretical DDHS, as schooling behavior affects all activities such as feeding, reproduction, migration and avoidance of predators. Formation of schools is also important for fishing, and this topic will be reviewed in detail in following chapters.

Most of what follows with respect to anchovy is based on MacCall's (1984) original work in models of habitat selection and egg and larvae as indicators of adult distribution.

Expansion Patterns : The Northern Anchovy

The northern anchovy central subpopulation is an important fishing resource for both commercial and recreational fisheries in the U.S. (California) and México (Baja California Norte). The central stock extends approximately from 38° N at San Francisco Bay, to 30° N at Punta Baja, Baja California in the south, but the bulk of the central subpopulation biomass is consistently located in the Southern California Bight (SCB), an area bounded by Point Conception, California in the north to Point Descanso, Baja California, in the South (PFMC 1984). The harvest from the commercial fleet is used almost completely for reduction and production of fish meal and fish oil and a small percentage is destined to canning for human consumption. There is also a very important recreational fishery in Southern California and Northern Baja California, targeting mainly on large predatory species which uses the anchovy as live bait, making this coastal bait fishery in some years economically even more important than the reduction fishery. The importance of this population is twofold because anchovy are also a major food item of many southern California desirable game and commercial species.

There is a large amount of data related to the fishery and its environment collected by monitoring programs since the early 1950's, when the Pacific sardine fishery collapsed. For example, the California Cooperative Oceanic Fisheries Investigations (CalCOFI) Program has monitored abundance and distribution of northern anchovy larvae and oceanographic variables off California regularly since 1951. The fishery itself (live bait and reduction) has been monitored regularly by State and Federal agencies both in México and in the USA.

Expansion and Contraction

Anchovy larval abundance shows a variation of 30 fold over the period studied, while estimated egg production shows a 1000 fold variation over the same period (Lo, 1985). These changes in egg and larvae abundance have been accompanied by large changes in distribution. This extreme variability and dynamic range in abundance and distribution is a cause of concern for management agencies (MacCall *et al* 1983) and may be an important factor in explaining why these clupeoid populations tend to easily collapse under exploitation (MacCall 1976, Lasker and MacCall 1983).

Larval Distribution

The larvae distribution maps in Figure 6 show changes in abundance for several years during the 1950's and 1960's. All surveys were conducted approximately at the same time in April, which is the historical period of peak anchovy spawning. The anchovy spawning population was increasing during this period from a low of approximately 3,200 tons in 1952 up to a moderate biomass of 421,000 tons in 1963. There was no substantial fishery during those years, except for the period from 1952 to 1957 (Table 2), probably caused by the final decline of the sardine fishery. The maps show the increase in both the range and the total area occupied by arbitrary levels of larval abundance. The medium density (100 to 1,000 larvae per 10 m² of sea surface) and high density (1,000 to 10,000 larvae per 10 m² of sea surface) levels are of particular interest.

Biomass estimates are uncertain during the early 1950's (harvest is higher than



Figure 6. Relative abundance of anchovy larvae in the California Current System. From Kramer and Ahlstrom (1968).

the estimated biomass in Table 2), but the spatial data shows that in 1952, larvae were located mostly near Santa Barbara, close to the coast, and the total area occupied in the Southern California Bight (SCB) was also small. The estimated spawning biomass of 3,000 tons this year was the lowest on record. When the spawning population increased by a factor of ten in 1956 to 27,000 tons, the range and the total area occupied expanded to include Northern Baja California. A further increase in biomass to almost 68,000 tons in 1957 caused the medium density distribution to extend offshore, and the range extended to the south of Pta. Baja. The higher density level is evident for the first time at isolated spots and coastal areas of the SCB, in the center of the distribution. A doubling of the spawning biomass to 120,000 tons in 1961 produced a largely expanded offshore distribution with several high density isolated spots in the SCB. The medium density distribution stretches now over a much larger area. When the spawning biomass reached more than 400,000 tons in 1963, larval distribution extended as far north as San Francisco. The high density larval distribution no longer consists of isolated spots, but now includes a large proportion of the SCB and extends continuously far offshore.

In general, the medium density level shows a change in location, but always within the geographical area of the Southern California Bight (SCB), which is roughly the accepted range of the anchovy central subpopulation. Also, the restricted geographic distribution and apparent geographical separation of the spawning products of the central and southern subpopulations is noticeable in the larval distribution.

Finally, Figure 7 shows the larval distribution in January-February 1975, year during which both the highest California harvest (149,377 tons landed; 55,271 tons landed in Mexico) and the highest spawning biomass ($3,642 \times 10^3$ tons) were recorded. The high density abundance level now is distributed over most of the spawning range, and there are isolated spots with very high concentrations (10,000 to 100,000 larvae per 10 m^2 of sea surface). The relative geographic distinction between the northern and the southern spawning centers is no longer evident. The high density level is almost continuous as far south as south of Pta. Eugenia. The overall area occupied is much larger, but the offshore boundaries seem to be similar to those reached at the spawning biomass of half a million tons. There is only slight spawning activity detected north of Pt. Conception.

Table 2. California anchovy landings and Spawning Biomass 1951-1985. Total landings include commercial landings for reduction purposes and live-bait catch. Landings 1951-1980 from PFMC (1984); 1981-1985 (*) Richard Methot, SWFC, Comm. Pers. Spawning biomass 1951-1979, low 1978 biomass egg production estimates from MacCall and Methot (1983) and 1980-1985 (•), direct egg counts from Hewitt (1985).

Year	Total Landings (metric tons)	Spawning Biomass (1000 metric tons)
1951	7,819	2.24
1952	31,481	3.20
1953	44,733	12.12
1954	25,302	31.10
1955	25,829	58.38
1956	31,563	26.97
1957	22,121	67.37
1958	9,106	235.57
1959	7,551	183.43
1960	6,519	326.53
1961	8,862	120.77
1962	6,849	243.12
1963	6,103	420.81
1964	6,966	767.13
1965	8,246	743.38
1966	34,394	972.18
1967	36,473	989.00
1968	20,740	345.01
1969	66,253	706.87
1970	92,853	512.38
1971	46,864	501.65
1972	67,994	306.55
1973	125,966	2621.65
1974	80,166	1472.80
1975	149,377	3642.41
1976	119,529	927.38
1977	107,541	1567.60
1978	17,470	431.61
1979	58,608	1003.78
1980	53,958	870.00
1981	56,234 *	635.00 •
1982	49,027 *	415.00 •
1983	8,487 *	652.00 •
1984	7,004 *	309.00 •
1985	5,282 *	521.00 •

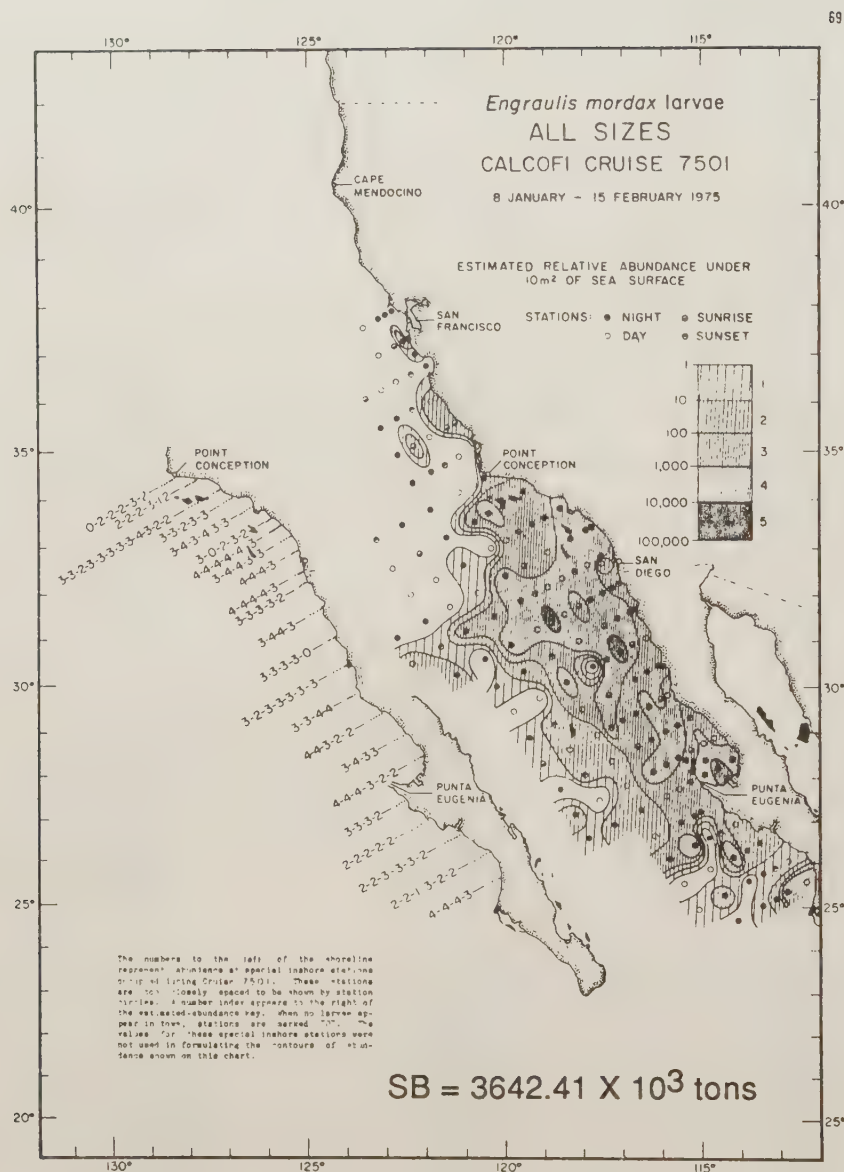


Figure 7. Anchovy larval relative abundance in 1975. According to MacCall and Methot (1983) spawning biomass was 3642.41 x 1000 metric tons. From Hewitt (1980).

The geographic variation of a density level in the distribution maps (Figures 6 and 7) agrees qualitatively with the Stern Stele conceptual model of Taylor and Taylor (Figure 1, Introduction). However, it is important to note that variation of density in highly suitable locations (e.g. those within the coastal SCB) is large. This variation was discussed by MacCall (1984) in relation to a geographic distribution model derived from larvae counts, and concludes that it accounts for most of the variation in total abundance, while expansion and contraction of range account for only a smaller fraction.

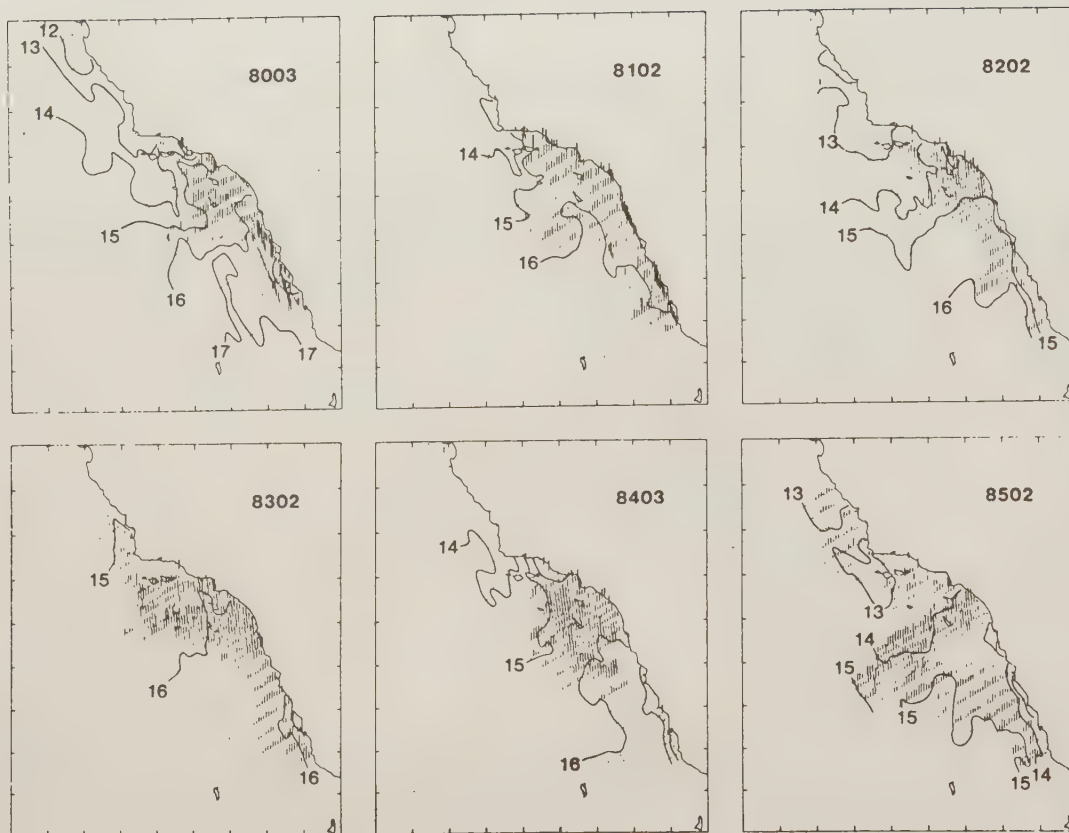
However, a qualitative comparison is difficult due to the many assumptions involved and to sampling problems. Some of the sampling problems include the tendency of small larvae to be extruded during the sampling operation, and the tendency of large larvae to actively avoid the net. More importantly, in comparing directly the maps it is assumed that the distribution of larva abundance is proportional to the distribution of adult abundance. However, mortality rates of egg and larvae are to a great extent dependent on larval abundance, so that the standing stock of larvae may not be directly proportional to the initial number of larvae or to changes in adult abundance over several years. Nevertheless, these distribution maps of anchovy larvae show some of the characteristics of an expansion cycle, which agree in general terms with the conceptual models.

Egg Distribution

From 1980 through 1985 the Southwest Fisheries Center in La Jolla, California, conducted egg production surveys during the peak of spawning to estimate anchovy biomass; both anchovy eggs and adults were sampled during the cruises. Details of the survey and techniques can be found in Lasker (1985). The resulting egg distributions are shown in Figure 8 and the adult distributions from night mid-water trawls are shown in Figure 9.

Some expansion and contraction changes can be observed in the maps, but the patterns are not very clear because there were no large changes in spawning biomass during the period. Under these circumstances, egg distributions may be more correlated with environmental changes such as water temperature than to actual total abundance.

The largest change in biomass occurred during the years 1983 and 1984, a



EGGS PER
0.05 M²

10 |
100 |
1000 |

Figure 8. Anchovy egg distribution and sea surface temperature in the California Current System 1980 - 1985. Paul Fiedler, SWFC, La Jolla. Pers. Comm.

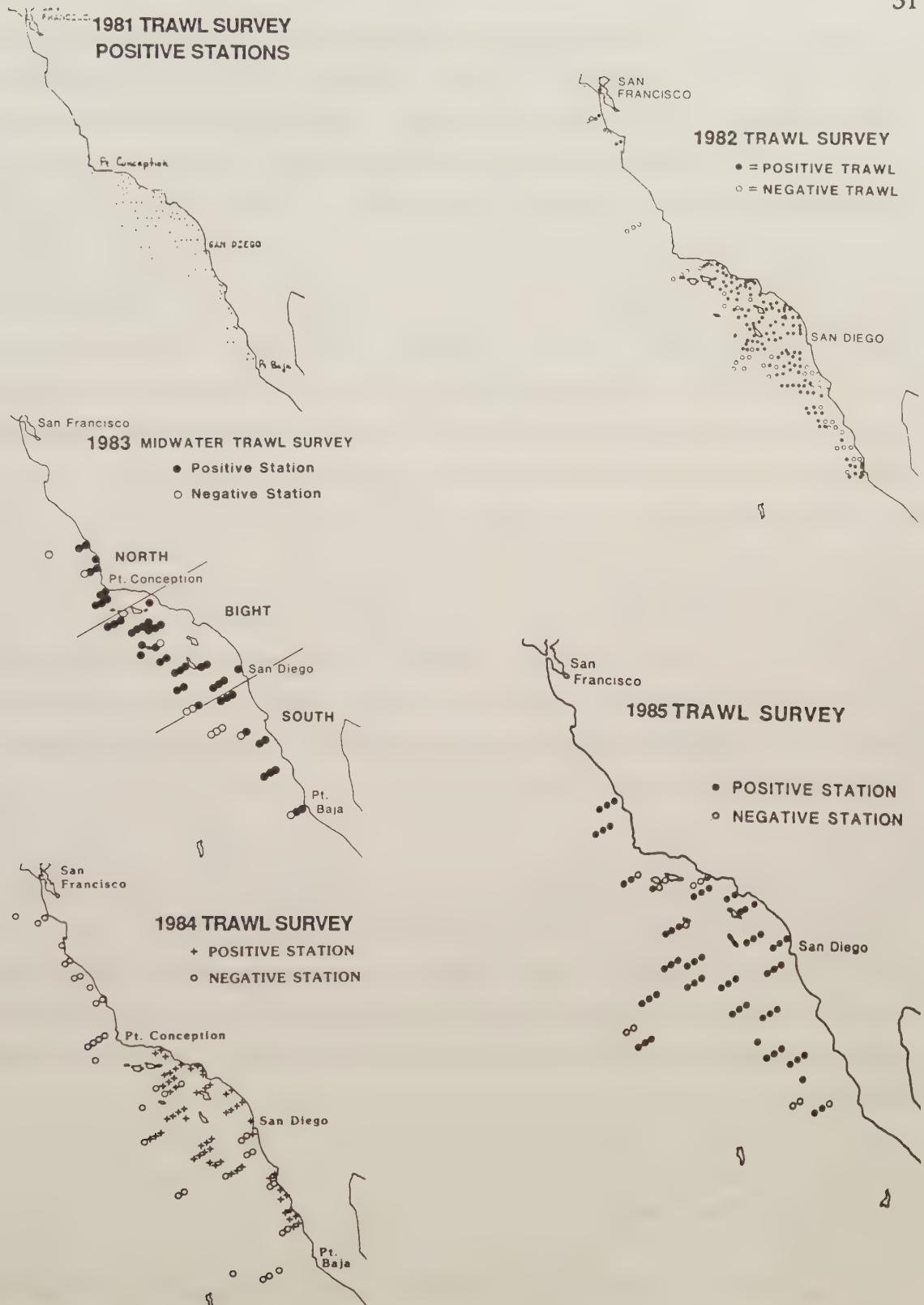


Figure 9. Geographical distribution of trawl sampling effort and trawls that caught adult anchovy. Positive stations/trawls are those in which adult anchovies were caught. Richard Charter SWFC, Pers. Comm.

decreasing in abundance from 652,000 tons to 309,000 tons. Some differences can be observed these years, particularly in the southern part of the range. This area has many spawning adults and eggs during the year of relative high abundance, but it is not occupied during the year of relative low abundance. The offshore spawning is somewhat more evident during 1983, particularly in the northern portion of the SCB, with some spawning around Pt. Conception. However, during the spring of 1984 this region registered temperatures of less than 15° C, and no spawning was detected in the area. In both years almost no spawning activity occurred in waters with temperature above 16° C, or below 15° C, particularly in the nearshore Baja California area. Adult distributions matched egg distributions in both surveys, and this was the case for all the years surveyed (Figure 9). The range and area occupied during spawning seem to be very similar for all surveys, with the main evidence of apparent contraction of range being the lack of eggs in the southern end of the distribution when the biomass was low and the apparent willingness of adults to spawn in slightly colder waters during the high abundance years. It can be argued that egg spatial distribution is closer than larva distributions to the adult spawning locations, because they are closer in time. However, spawning distribution is not only affected by adult abundance but also by water temperature and circulation, which caused an apparent offshore spawning in 1985 as a result of entrainment by an offshore gyre.

As can be seen from the above examples, not only the overall distribution of anchovy eggs, larvae and adult changes, but also the variability at locations of supposedly high suitability is large. This can be an indication that the distribution not only expands and contracts in response to abundance levels, but also shifts its center and changes form and total area, probably as a response to environmental forces.

Ideal Free Distribution

A quantitative analysis and a partial test of the Ideal Free Distribution (IFD) using northern anchovy egg and larvae data has been made by MacCall (1984). Habitat suitability is defined as the marginal component of reproductive value

conferred by the selection of a particular habitat. If fecundity is measured in terms of offspring surviving to a certain age, then the mortality rates of eggs and larvae will be a large component of reproductive value. The IFD predicts that all individuals will distribute among habitats in such a way that all occupied habitats are equally suitable. Therefore egg mortality rates should be similar in all habitats occupied by the spawning anchovy.

Using counts derived from the 1982 egg production survey (see Figure 8) three areas of varying egg abundance were defined: two areas of high abundance, one off Southern California and one off Northern Baja California, and the rest of the survey area, with low density. Subsequently, egg mortality rates were estimated by linear regression of the log-transformed abundances at age. The egg mortality rate estimated from the low density region was smaller than the estimates of the two high density regions, but when corrected for transport of eggs due to the California Current System, the estimates were more similar. A more complete test of the hypothesis of equal mortality is not possible, but it is highly likely that egg mortality rates are similar among areas. MacCall's study concludes that the distribution conforms to the IFD predictions, particularly taking into account the limited sensory capacity and delayed movement of anchovies which may make the animals never recognize fully the density dependent deterioration of the habitat. This circumstance may make the animals to behave "imperfectly", approaching the IFD without ever quite reaching it.

Furthermore, using a model of anchovy larval distribution constrained by the IFD, MacCall (1984) was able to map the probable extension of the larval habitat for several levels of spawning biomass. The Ricker spawning-recruit model usually applied to entire stocks is used to describe dynamics in the local habitat. According to the IFD (see above), mortality rates of larvae are assumed constant over habitats. An index of adult abundance in various habitats is linearly related to counts of 8 mm larva, standardized and scaled to adult abundance per year. The parameters of a generalized model are then estimated using the larval data. This formulation allows to estimate the approximate larvae "nominal edge" distribution for varying levels of adult abundance (Figure 10). At spawning biomass below 2,000 tons the range should contract into the few most favorable locations, while at the estimated unfished equilibrium biomass of 1.9 million tons (MacCall and Methot 1983) spawning would extend over an area of $250 \times 10^9 \text{ m}^2$, with a range covering from San Francisco to Punta Baja and extending considerably offshore.

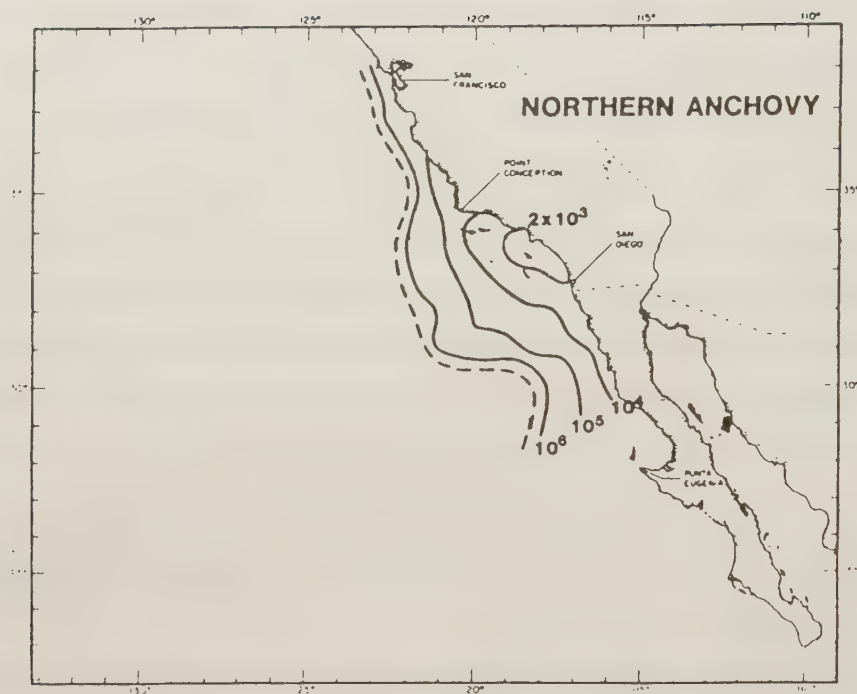


Figure 10. Approximate anchovy spawning habitat suitability contours. Distribution of larvae at different spawning biomasses. At low levels of spawning biomass, larvae are restricted to the nearshore areas of the Southern California Bight; the dashed line is the limit of larvae distribution at estimated population carrying capacity of about two million tons. From MacCall (1984).

As expected, the spawning suitability contours are qualitatively similar to the actual larval distributions (see Figures 6 and 7) especially at low abundances, as the contours were derived from larva abundance data. However comparisons and the use of distribution maps to investigate Density Dependent Habitat Selection should be made with caution due to the many sampling errors and assumptions involved. Some of the most important assumptions include:

- Sampling error due to initial patchy distribution of eggs and larvae and subsequent dispersion away from the spawning location; high biological viscosity, e.g population may not have achieved the IFD by the time of spawning.
- Variable fecundity, i.e. lack of proportionality between larval abundance and abundance of adults and no linearity between habitat suitability and spawner or larval density.
- Variability in the perception mechanism or “clue” the animals use to assess decreased density dependent suitability, i.e. effects of food abundance, as the diet of larva and adults overlaps to some extent, and feeding conditions may be one of the clues used to select the habitat.
- Correlation of the distribution with density independent environmental factors, i.e. water surface temperature seems to limit anchovy spawning activity in the north of the range of the central subpopulation (Lasker *et al* 1981), and salinity seems to restrict spawning in the south (Stauffer and Picquelle 1980), at least at moderate levels of abundance.

The violation of these assumptions would probably affect the analysis of the anchovy distribution as an example of IFD. However, the qualitative results remain the same; therefore it is very likely that the northern anchovy range expands and contracts with changes in density.

Contraction Patterns : The Pacific Sardine and the Peruvian Anchoveta

Pacific Sardine

The Pacific sardine (*Sardinops sagax caerulea*) was the object of an important fishery along the West coast of North America. The catches peaked in the late 1930's and subsequently declined until the late 1960's when the population abundance decreased to a point of commercial and almost biological extinction. The fishing effort increased, also peaking in the late 1930's, remaining approximately constant throughout the 1950's and declining during the 1960's (but see MacCall, 1979, for a revision of Murphy's (1966) estimates of effort, landings and biomass). The fishery was sustained by two genetically distinct races with some spatial but limited temporal overlap: the northern race, larger and with a smaller rate of natural mortality, ranging from British Columbia to southern California ; and a southern, smaller race with higher rates of natural mortality, ranging from southern Baja California to approximately San Pedro, in the SCB.

The early increase in landings (peak of approximately 800,000 tons in 1937) can be attributable to increased fishing effort, but the subsequent decline is probably related to a declining population. Murphy (1966) has proposed that the following sequence of events contributed to the commercial extinction of this species:

The decline in abundance and subsequent reduction in catches began in the Pacific northwest and British Columbia and it is attributable to the decline of the northern segment of the population. During two consecutive years there was a reproductive failure, which produced few recruits to the fishery, diminishing the number of individuals participating in the northern migration. The population collapsed when heavy fishing changed the age structure of the population, leaving a less than adequate proportion of old individuals that, according to Murphy (1966) were the reproductive "insurance" needed to counterbalance the effects of an adverse environment on reproduction. The result of this ecologically unsatisfactory age structure was the almost complete cessation of exploitation in the northern fishing grounds, and a behavioral response from the sardine population. This response was the contraction of spawning range, probably related to Density Dependent Habitat Selection and the IFD. The center of spawning activity also

changed, shifting to the south after the decline of the northern segment of the population. The fishing grounds also were reduced (Felin 1954) following the contraction in spawning areas, but the catch per effort indices did not show a declining population in Southern California, which was the most active fishing area at the time. This pattern of contraction of range, shifting of spawning center to the south and contraction of fishing areas continued until the commercial (and almost biological) extinction of the Pacific sardine in the late sixties.

Parallel with these changes, the northern anchovy population increased during the fifties (see Figure 6 on anchovy section above), presumably filling the ecological void left by the sardine. This prevented the latter population from increasing again, since both species share to some extent the same resources, although probably not competing directly (but see Maccall, 1979 and the general review by Daan, 1980; there is no conclusive proof of substitution of sardine by anchovy). According to Murphy (1966) the combination of these events produced the decline of the sardine population beyond capacity of recover.

Fishing activity

The shifting of the fishing center to the south, paralleling the shifting in spawning can be seen in Figure 11. The range of the population extended from British Columbia to Southern California during the peak of the fishery in the late 30's. Fishing ceased in Canada after the 1947 fishing season and stopped in Washington and Oregon after the 1948 fishing season. According to Murphy (1966), at this point the southern segment of the population began to dominate the fishery, which had been until then dominated by the northern segment. Biomass (age two and older) was around 500×10^3 tons that year (see Figure 12). Fishing continued in more southern grounds such as San Francisco until 1951 when significant landings began also to be reported from Baja California (most of them were probably individuals from the northern segment). In 1951 the biomass (age two and older) was down to 277×10^3 tons from 780×10^3 tons in 1950. The Monterey fishery declined drastically after 1959, when biomass was at 122×10^3 tons, but some small landings were reported in Northern California until 1965. Throughout the fifties fishing continued in Southern California and Baja California, but by the mid sixties landings in both areas had declined substantially and the population biomass was down to only 3×10^3 tons in the late 1960's, when all commercial fishing was stopped. Biomass at this point was probably at an all time low.

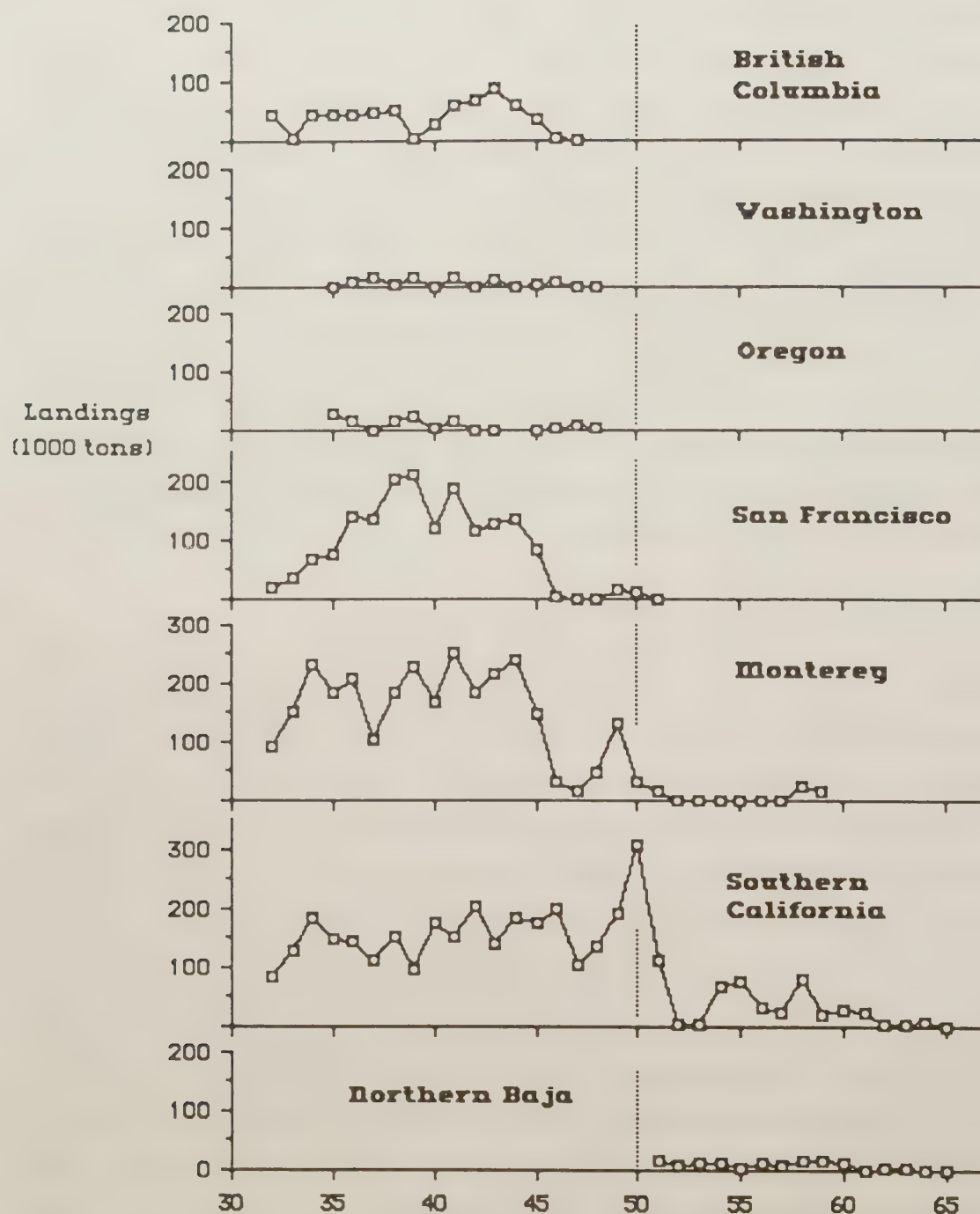


Figure 11. Sardine landings by region 1932-1965. No landings were reported from the northern range by the late 40's, while the catch peaked in Southern California in 1950. From Murphy's (1966) landings data.

Biomass (age 2 and older)
(1000 tons)

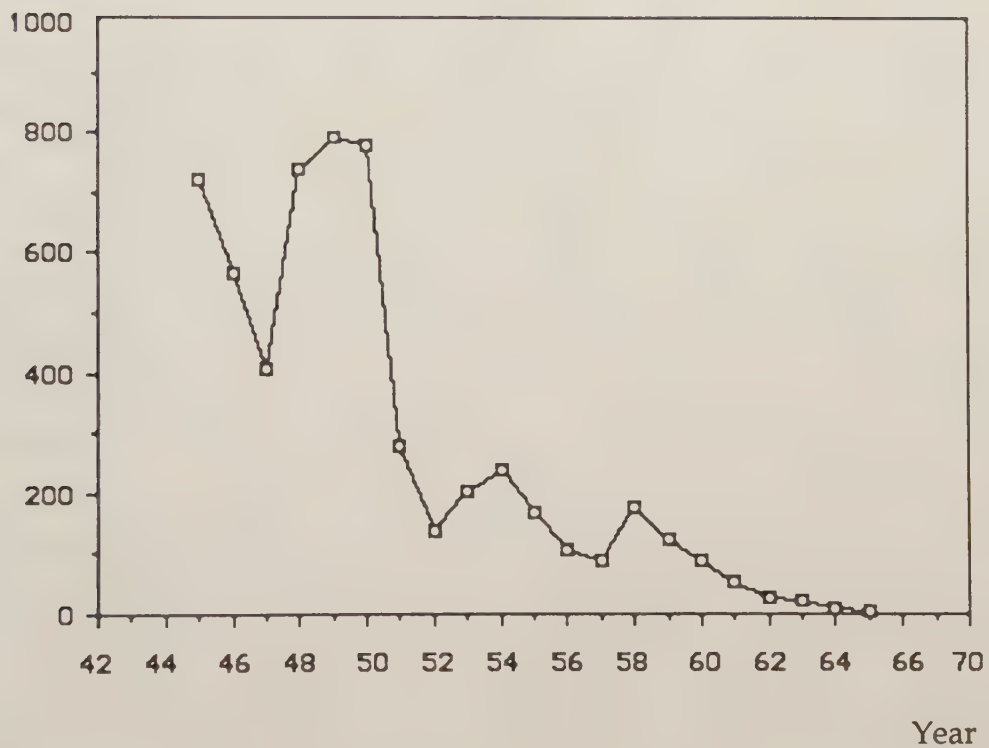


Figure 12. Sardine biomass (age 2 and older) 1945-1965. The largest decline was observed during the early fifties, immediately after the landing record of 1950 in southern California. From MacCall's (1979) data.

Egg Distribution

This contraction-shifting pattern can also be observed in the egg distribution maps shown in Figure 13. These maps are analogous to those presented for anchovy larvae in Figures 6 and 7, and were prepared using the same CalCOFI data. All maps show the egg distribution for April-May, approximately the peak of the spawning season for the central portion of the population in those years (Murphy 1966). The period considered is from the early fifties to the mid sixties, when the sardine population abundance (fish age 2 and older) was decreasing (Figure 12).

The year 1950 was the last with a moderate biomass, estimated at 780×10^3 tons. There was a sharp decline in biomass during 1951, when only 277×10^3 tons were estimated, and this signaled the final decline of the sardine population abundance (MacCall 1976). The area of spawning reflected by egg distribution, was fairly large encompassing south of SCB and north of Baja California, but spawning activity was light, with only a few positive stations within the SCB. There is a center of high egg abundance (1000 to 10,000 eggs per 10 m^2 of sea surface) around Pta. Eugenia, in the southern range. During 1952 both biomass (136×10^3 tons) and spawning area decreased, but increased again slightly during the next two years. During 1954 biomass was 239×10^3 tons which produced the occupation of a fairly large area. There is some medium (100 to 1000 eggs per 10 m^2 of sea surface) to high activity detected in the SCB with some stations yielding eggs in the offshore region. The southern area of spawning is predominantly centered north of Pta. Eugenia. This was the last year eggs were sampled in high concentrations and over a large range. Biomass continued to decline and the range of spawning continued to shrink after this year. During 1955 the northern and southern areas of spawning were isolated, and spawning was in general lighter, but centered in the same areas of previous years. A more fragmented pattern started in 1956, when the biomass decreased to 108×10^3 tons. The center of spawning was offshore of the SCB, with medium and high density detected at several stations. The southern center was located in the coastal area near Cedros Island. An even more fragmented and coastal egg distribution was characteristic of subsequent years, and the biomass continued to decline, despite a slight increase in 1958 (177×10^3 tons). Spawning became very restricted to the coastal areas of the SCB during 1959, but intense at a few places, and the biomass was down to 122×10^3 tons. When biomass falls below 100×10^3 tons throughout the

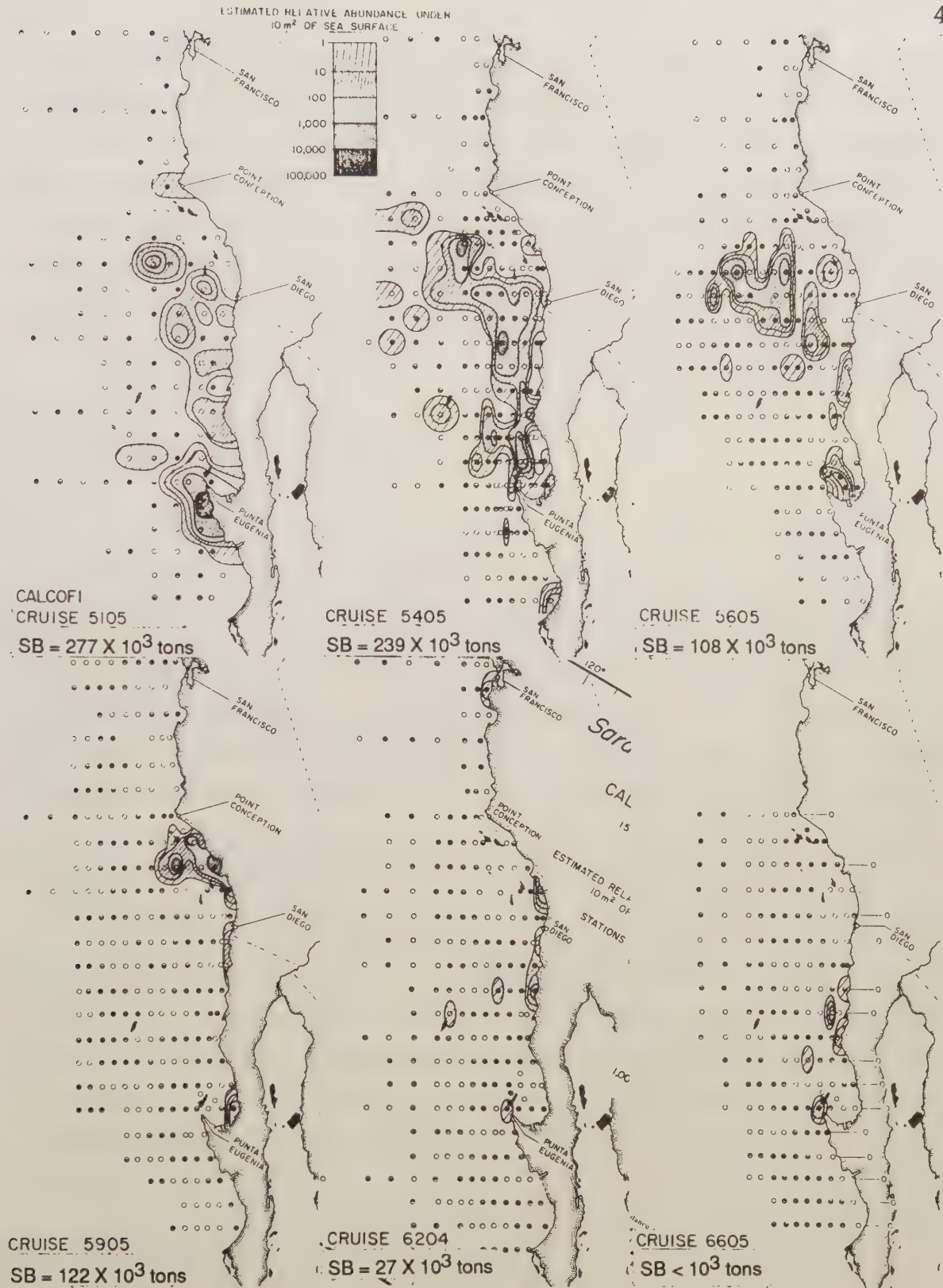


Figure 13. Pacific sardine egg distribution. The population abundance decreased and shifted South from 1951 to 1966. From Kramer (1970).

late fifties and early sixties, egg distributions become discontinuous and sampling problems make more difficult to interpret the maps, but in general spawning area continued to shrink producing coastal and isolated egg distribution patches. The southern spawning area almost disappeared after 1956 and the northern egg distribution area became very patchy with only a few positive stations in the SCB. By 1966, with a biomass of less than 10,000 tons remaining, there was no spawning activity detected within the SCB during the CalCOFI surveys. Population range and distribution had been fragmented, with only a few isolated pockets remaining in the southern range.

Peruvian Anchoveta

Another case of a contraction pattern with decreased abundance can be documented for the Peruvian anchoveta (*Engraulis ringens*). This species has undergone large changes in biomass and recruitment, many of them related to environmental factors such as El Niño, which is the collective name for a series of environmental changes mostly associated with the abnormal warming of large areas in the Pacific Ocean, affecting climate worldwide. However, abundance changes have also been related to fishing pressure and biotic interactions.

Exploitation of this species was small prior to the late fifties, increased rapidly during the sixties, and developed in only a few years as the largest single species fishery in the world. From 1960 - 1970 the average landing was 7.8 million tons, with a maximum of 12.3 million tons in 1970. This quantity accounted for 20% of the world total catch during the year. After 1971 landings decreased drastically, down to approximately 1.0 million tons during the late seventies. The anchoveta biomass decreased from a high of over 25 million tons during 1967-1968, to levels below 1.5 million tons by 1981 (Santander *et al* 1984), probably as a consequence of intense fishing pressure and the reproductive failure (due to environmental changes in critical years) of a large segment of the population.

The history of both the fishery and the environmental and biological variations in the Peruvian upwelling system has been well documented, and it is especially complete after the 1971 collapse. Many general references can be found in Ricker (1973), Clark (1975), Murphy (1977) and Daan (1980). The fishery and the recent

increase in other pelagic species after the decline of the anchoveta has been documented by Tsukayama (1983) and Zuta *et al* (1983).

The range of the anchoveta extends over an upwelling area of 4000 km, from 4° 30' S to 42° 30' S, but the bulk of the population is concentrated mostly in the Peruvian coast between 5° S and 19° S. The offshore distribution is usually restricted to the coastal area of less than 100 km, and most of the fishery takes place within 10 km of the coast. The distribution is generally bounded by the 14° and 19° isotherms and by a low oxygen undercurrent layer below 40 m (Mathisen 1979). The largest concentrations of fish are usually found in Northern and Central Perú, but local density often varies sharply. Abundance drops abruptly north of the range, while it decreases gradually in the south.

Anchoveta in the pelagic environment

The expansion and contraction pattern has been observed in this population, but the density dependence of habitat selection and the center or centers of spawning seem to be heavily influenced by environmental changes and by the presence of other species. The decline of the population is shown in Figure 14. In this diagram the isolines indicate the catch (in percentage of total weight) of anchoveta relative to the catch of other pelagic species (sardine, *Sardinops sagax*; horse mackerel, *Trachurus symmetricus murphyi* and Pacific mackerel, *Scomber japonicus peruanus*) taking into account all exploratory fishing sets by season and latitude. The data come from IMARPE's (Instituto del Mar del Perú) exploratory fishing cruises from 1972 to 1983 (Zuta *et al* 1983). The graph in Figure 15 shows the estimated anchoveta biomass from 1963 to 1981 (Tsukayama 1983). The biomass estimates for 1963 to 1970 were obtained by the use of cohort analysis. From 1971 to 1981 the estimates are from hydroacoustic assessment cruises. These estimates should be considered with caution, especially those derived from cohort analysis, because there is strong evidence (see next section on clinal variation) suggesting that the natural mortality rates in coastal pelagic fish are not constant, as the method assumes.

The Figures show that biomass was very high from 1963 to 1970, fluctuating between 12 and 25 million tons, averaging around 17 million tons. Biomass declined abruptly during 1971 and 1972 down to 9 million tons and continued to decrease in 1973, when it was at 5 million tons. The spatial information shows that during 1972, particularly during the winter, the population was restricted to a coastal area

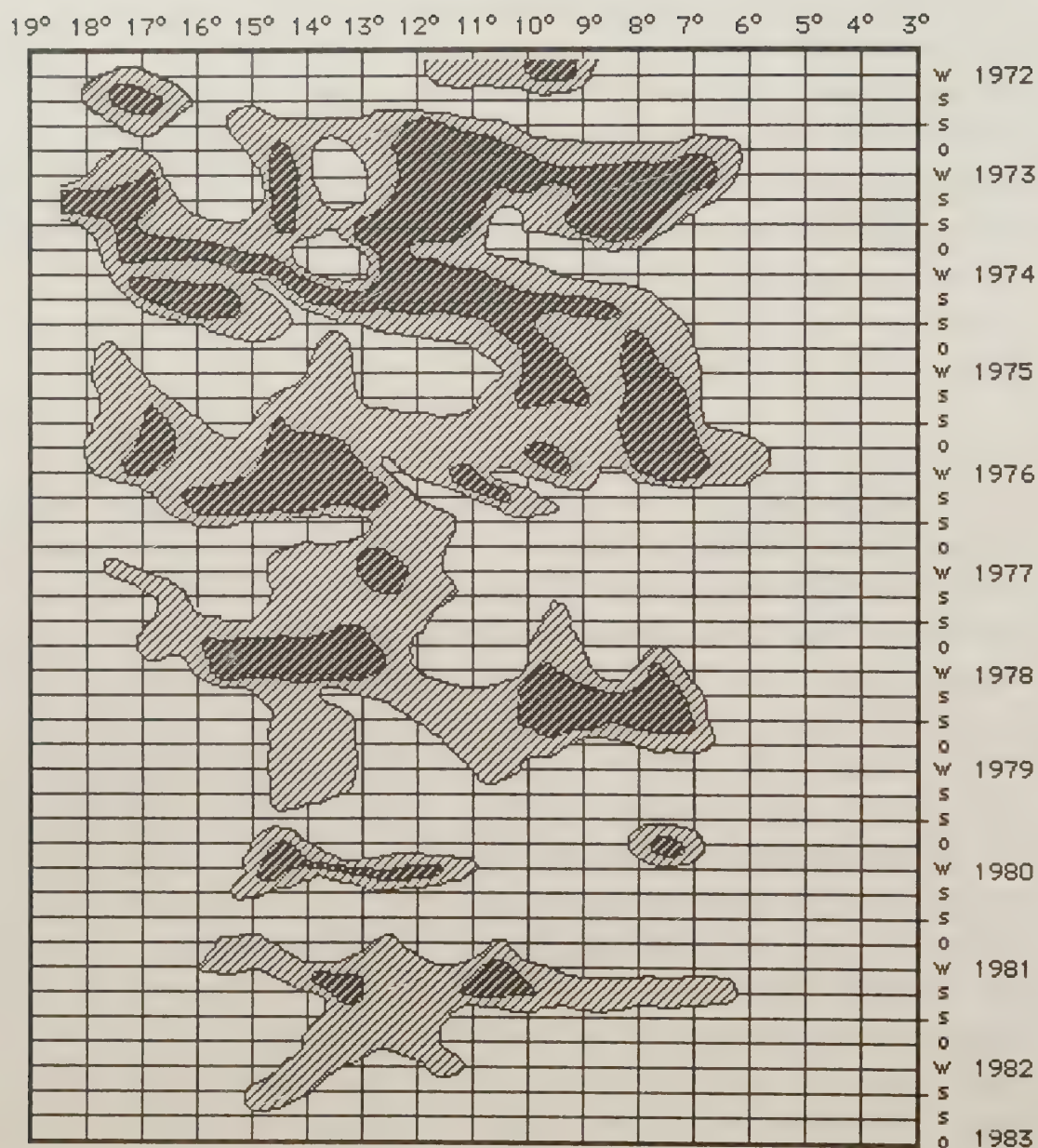


Figure 14. Seasonal and annual variation in the spatial distribution of the Peruvian anchoveta 1972-1983. Data are very sparse during 1977-1979, therefore the results are mostly extrapolations during these years. The anchoveta accounted for 30% to 50% of total weight of pelagic species in light shaded areas. Dark shade represents areas where the anchoveta weight was more than 50% of total biomass. Data are from IMARPE's exploratory fishing cruises. Redrawn from Zuta *et al* (1983).

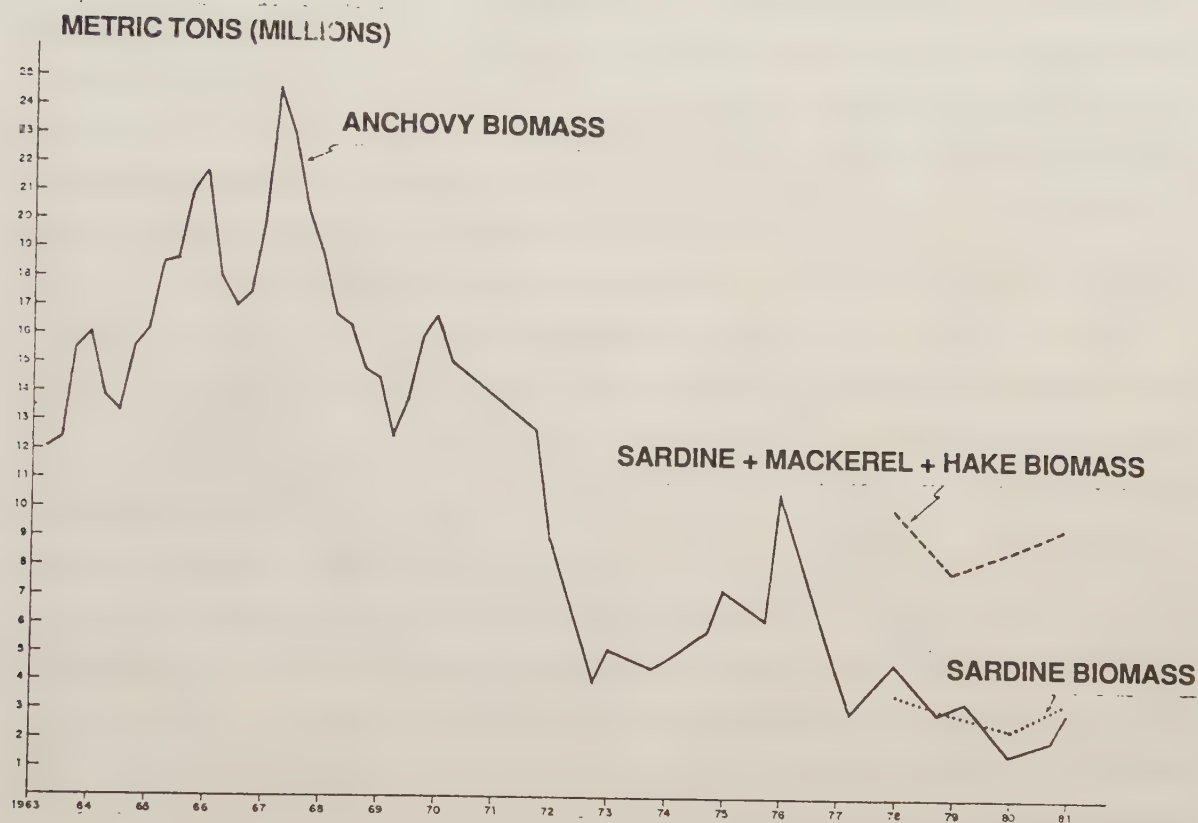


Figure 15. Seasonal and annual variations in anchoveta biomass along the Peruvian coast 1962-1982. From Zuta *et al* (1983).

between 9° and 12° S, and during the spring moved south to 17°. This distribution is probably associated with El Niño warming events, which were particularly strong during 1971 and 1972. In contrast, during 1973 and 1974 the anchoveta population occupied a large area, from 7° to 18°, with high proportions of anchoveta in the northern end of the distribution in 1973, despite the relatively low biomass of 5 million tons. During 1974 both biomass and the distribution are similar to the 1973 values, but relative abundance was slightly constrained and reduced, and somewhat shifted to the South. During the first part of 1975, the anchoveta distribution shows large gaps, with most of the fish concentrated in the northern areas. By the end of the year however, the biomass was up to 10 million and the distribution (centered around 14°) becomes almost continuous over a large area from 7° to 18°.

The last year a large biomass was estimated was 1975, since it declined steadily from 1976 to 1981, averaging less than 4 million tons. In these years the contraction of the range and the relative lesser importance of the anchoveta in the pelagic system becomes more clear. The same pattern detected in 1972 can be observed in a smaller scale during 1976, when the bulk of the population moved south of 13° as a response to El Niño of 1976 -1977. However, as can be seen in Figure 14, anchoveta biomass dominated the pelagic assemblages throughout the range this period. 1977 was a year of distribution restricted to the central area, and by 1978 the fish were found in the whole area, but in isolated pockets of dominance. During 1979 the distribution becomes more discontinuous, with only one patch of relative high dominance. The distributions for 1980 and 1981 are similar, showing large gaps and only a few places in the north and South where the anchoveta is still the dominant biomass of the pelagic species. The year 1982 had a more uniform distribution, but with low proportions of anchoveta in the pelagic communities throughout the range. The distribution during 1982 is probably related to 1983 - 1983 El Niño events, but the distributions from 1979 to 1981 are more attributable to changes in population size and biotic influences, since no abnormal sea temperatures were recorded those years.

Egg Distribution

The anchoveta egg distribution also shows the same general pattern of continuous distribution for periods of high total abundance and patchy, isolated spawning groups during years of low abundance (Figure 16). In 1967 the egg distribution is uniform in the central and northern areas, and the center of spawning seems to be

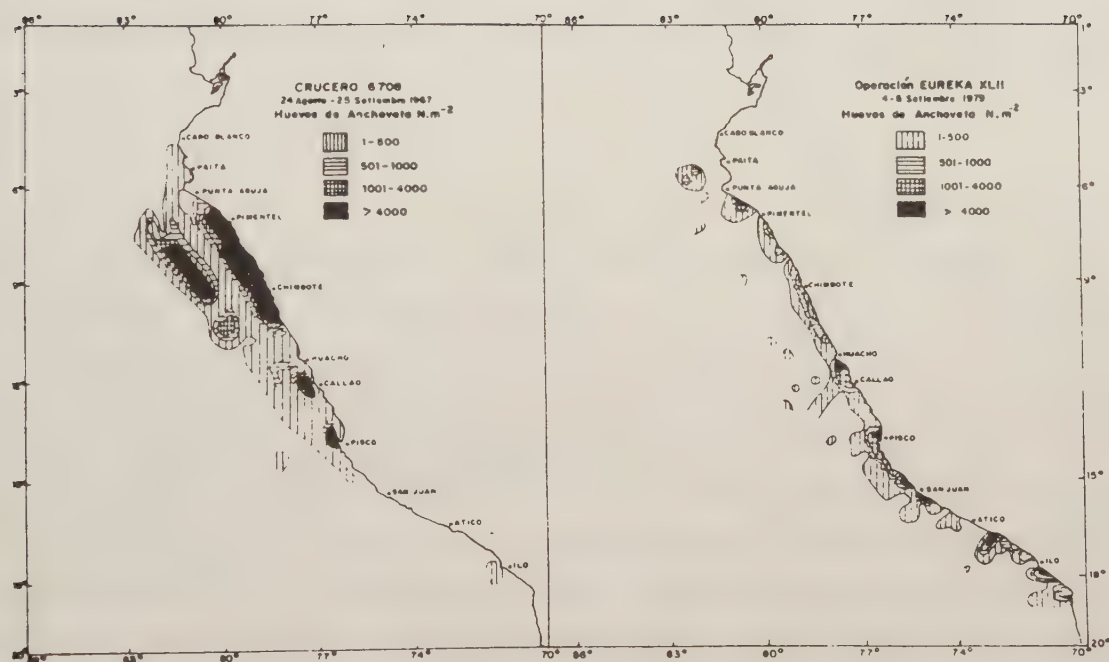


Figure 16. Geographic distribution of anchoveta egg samples in 1967 and 1979. The distribution is more fragmented and there are isolated regions of high concentration in the southern Peruvian coast during 1979. From Santander *et al* (1982).

around 8° S. There are also large concentrations of eggs offshore, and smaller pockets of high concentration in the central areas; almost no eggs were detected in southern Perú. Biomass was estimated at around 18 million tons in 1967. After the collapse of the fishery in the early seventies the egg distribution seems to be more fragmented and was shifted South (the Pacific sardine showed a similar pattern). Spawning now encompasses a large, discontinuous area, with no eggs in the offshore region. High egg abundance seems to be constrained to semi-isolated patches scattered over the range but distributed somewhat more compactly in the southern region. Biomass was probably around 3 million tons during 1979 (Santander *et al* 1982).

Hydroacoustic Data

Hydroacoustic assessment provides almost continuous coverage of an area and therefore it can provide some direct evidence on distribution. For example, hydroacoustic surveys were conducted for two consecutive years with different biomass (Figure 17). During 1976, the biomass was at approximately 10 million tons, and the area occupied by the anchoveta appears continuous along the peruvian coast, except for a small gap in the south. Local density however, varies along the coast, but anchoveta is the dominant fish species in the pelagic system that year. In the following year biomass decreased to less than 4 million tons, and the distribution becomes discontinuous, but maintaining approximately the same overall range as during the previous year. The individuals appear to be somewhat closer to the coast, and the southern end of the population has fragmented, with only two isolated pockets remaining. Distribution in both years might however, have been influenced by El Niño, especially during 1976, with the population moving slightly south to a more favorable environment. Nonetheless, the distributions seem to be strongly related to population size, because the high abundance year showing a large and continuous area of occupation, while the low abundance year shows a patchy distribution, with more gaps.

Finally, the graph in Figure 18 sums up information by showing a trend of decreased area occupied by the anchoveta from 1966 to 1979 for summer and winter distributions, estimated from hydroacoustic cruises. The general contraction trend agrees with the pattern of decreasing biomass abundance over the same time span.

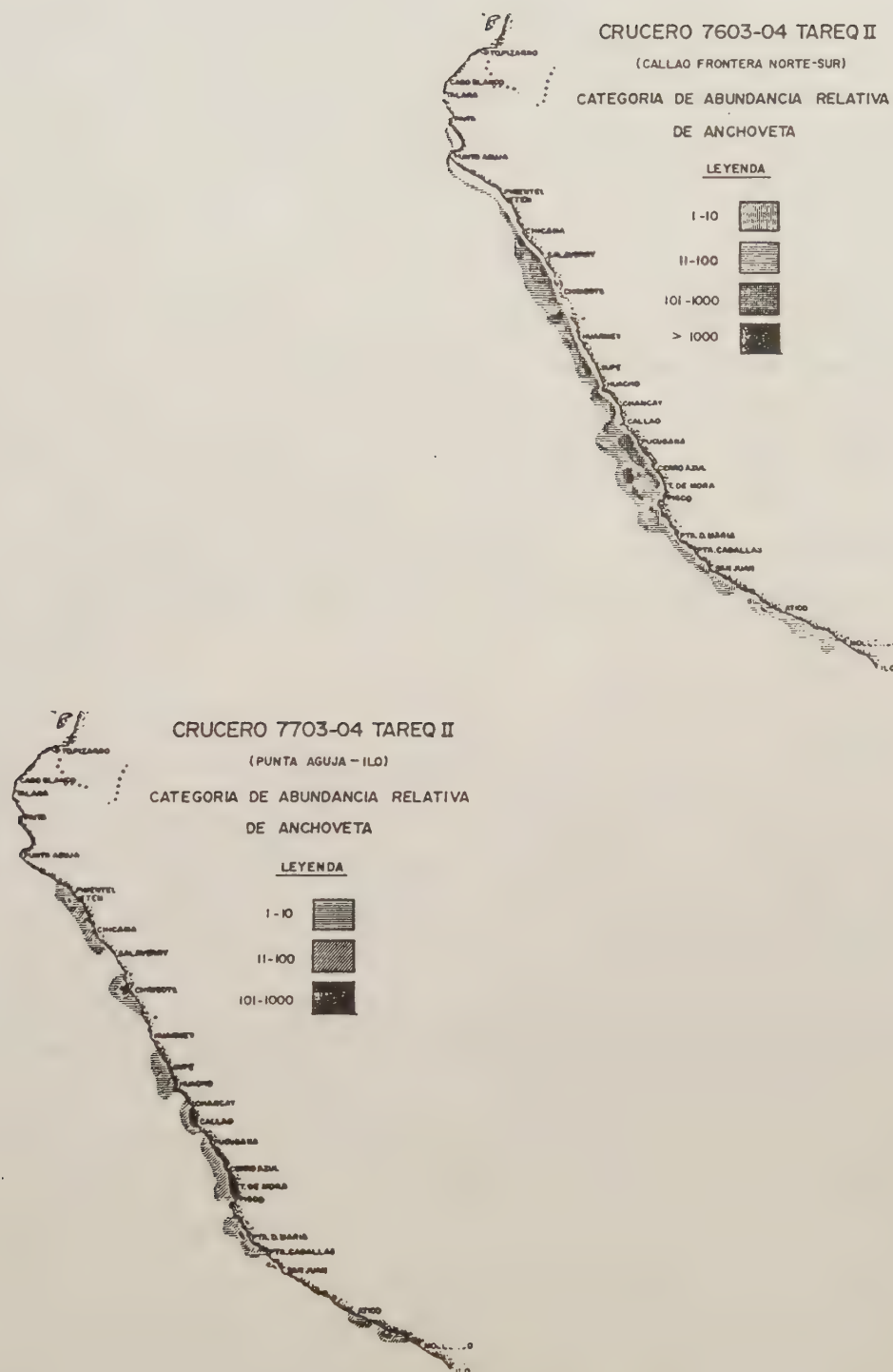


Figure 17. Relative abundance and distribution of adult anchoveta during hydroacoustic surveys in 1976 and 1977. The anchoveta population appears to be more dispersed and concentrated in isolated pockets during 1977. From Johanneson and Vilches (1981).

Area inhabited
(squared nautical miles)

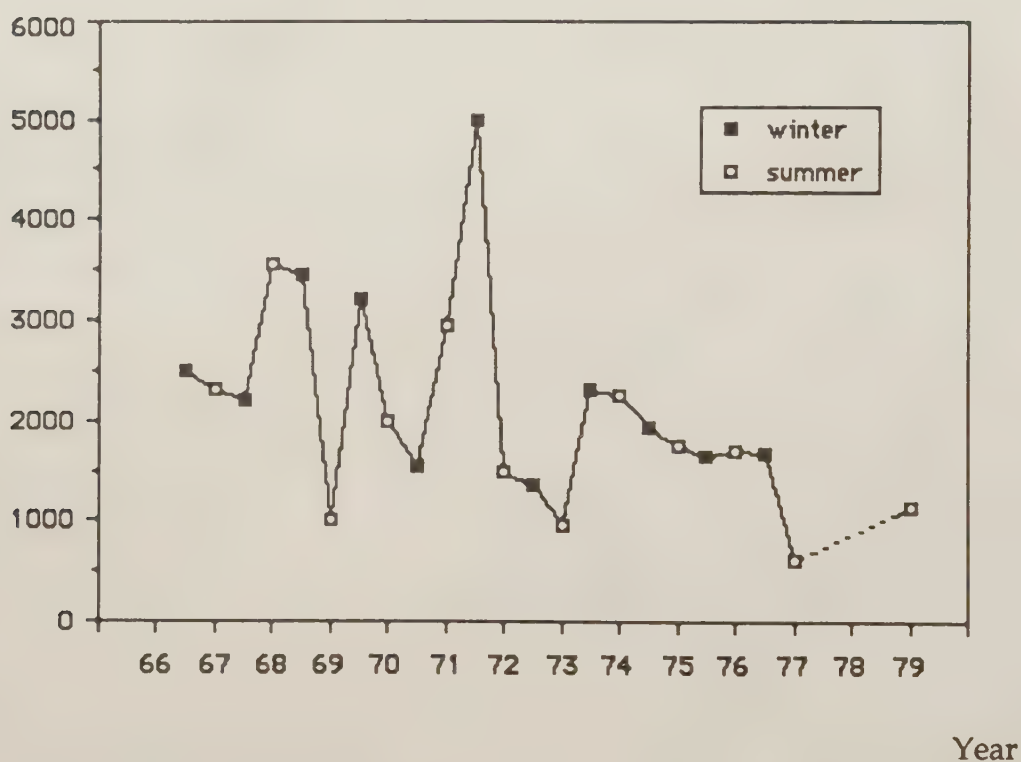


Figure 18. Changes in the extent of the area inhabited by Anchoveta 1966-1979. Areas are measured in average square nautical miles per latitude degree. The smaller values are registered after 1971. Hydroacoustic data redrawn from Zuta *et al* (1983).

The typical pattern during the high abundance years of the sixties was a population composed of loose schools and a widespread distribution in winter, extending up to 100-120 nm offshore. In contrast the summer aggregations were usually dense and confined mostly within the 40-50 nm coastal strip. According to Zuta *et al* (1983), this pattern was probably the result of environment and high overall abundance.

From the graph it is clear that after 1972, when the biomass decreased, the area inhabited does not exhibit the large seasonal fluctuation typical of the previous decade. At the same time it is also clear that there has been a reduction in total area occupied; the region inhabited now represents only 50% of the 1966 to 1971 distribution area. Also, Johanesson and Vilches (1981) report large oscillations in local density from 1973 to 1979. These changes in local density may well be related to the contraction and shifting of range. Exploitation seems to have followed the same pattern, concentrating in small areas of high local abundance (Mathisen 1979, Zuta *et al* 1983).

This brief review of the distribution of the Peruvian anchoveta shows clearly that the population exhibits expansion and contraction of range with changes in density, especially after 1972 and particularly after 1976 when the total biomass probably fell below 5 million tons. The reduction in area inhabited seems to produce several relatively isolated reproductive subcenters that have led Mathisen (1979) to propose that the population is to some extent composed of multiple units during the spawning season, but appears to be continuous at high abundance levels. One probable explanation of this phenomenon is that IFD is operating in these small centers; therefore the distribution expands at higher densities, appearing continuous due to the occupation of otherwise peripheral habitats, i.e. those away from the main upwelling centers.

However, it is not clear to what extent the peruvian anchoveta population conforms to the IFD, because the environment plays a major role in distribution, forcing individuals to move south during periods of warm water temperatures associated with El Niño. This shifting south appears to be somewhat independent of abundance since individuals may not behave "ideally" during this warm water periods.

Parallel Contraction and Expansion : Sardine and Anchovy

The contraction of range of the Pacific sardine and the parallel expansion of range of the northern anchovy can also be observed in the larval maps from Ahlstrom (1966) shown in Figure 19. During 1954, which was the last year the sardine population occupied a large spawning area, spawning activity was detected from south of Pt. Conception to the tip of the Baja California peninsula and biomass was estimated at 239×10^3 tons. A fairly large, continuous area of high larval density (1000 to 10,000 cumulative totals) extends from offshore SCB to the lower central portion of Baja California. Three isolated spots of high density larval concentration are detected: one slightly south and offshore of Cape San Quintin, one offshore of Pta. Eugenia and the last one in the upwelling areas of the lower Central Baja California. In contrast, the 1962 larvae distribution is discontinuous, with only a few isolated patches of low larvae concentration remaining within the SCB. There is some spawning around Pta. Eugenia, but it is not as strong as in other years. During this year biomass was estimated at only 31×10^3 tons for the area north of Pt. Colnett, the lowest level recorded to that date. Contraction of larval distribution range is clear and encompassed an area of thousands of km^2 .

On the other hand, anchovy larvae distribution is continuous from north of Pt. Conception to lower Central Baja California in 1954, when the spawning biomass was 31×10^3 tons. The coastal areas throughout the range have high larval density levels, but the anchovy larvae do not occupy the offshore region as extensively as the sardine larvae. By 1962 this high density level had expanded considerably, particularly offshore of the SCB. Larvae were detected as far north as San Francisco, and the offshore, presumably marginal area is now occupied extensively, probably influenced strongly by transport due to the Southern California gyre, but extending nonetheless over a larger area. Anchovy spawning biomass was estimated at 243×10^3 tons for this year.

The differences in relative abundance and distribution for these two years are much higher for the sardine than for the anchovy. The relative abundance is also higher for the anchovy, even during 1954, but this pattern was observed even before the Pacific sardine abundance decreased to low levels, i.e. during the early 40's the

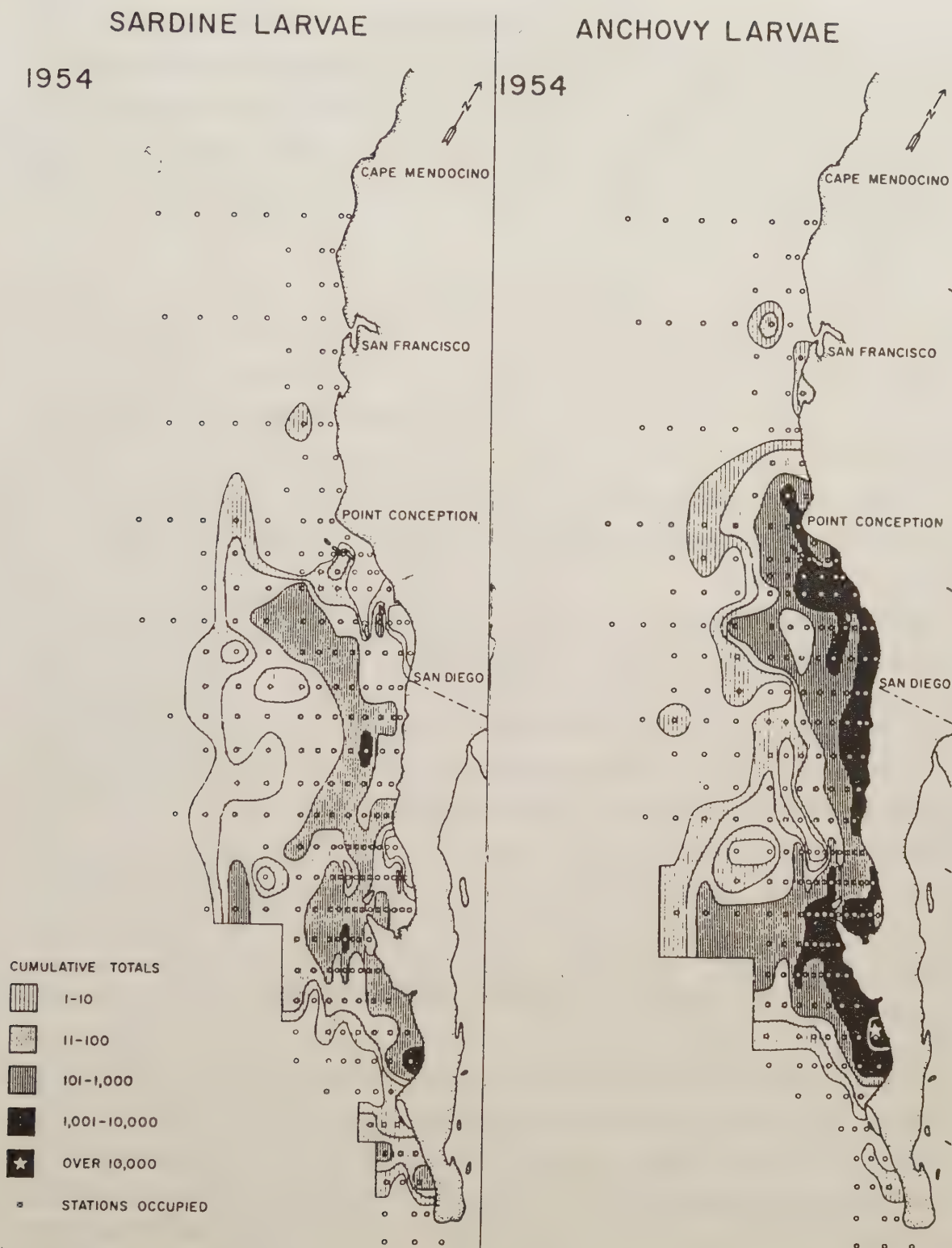


Figure 19. Distribution and relative abundance of sardine and anchovy larvae in 1954 and 1962. The sardine larvae shows a clear reduction in the extent of the area occupied at low population biomass levels. From Ahlstrom (1966).

ratio of anchovy to sardine larvae abundance was approximately 1.2 to 1.0 (Ahlstrom 1966). It should be noted however, that although there is some evidence that both species compete to some extent, there is no conclusive proof that the anchovy population competitively replaced the sardine, as both populations tend to occupy somewhat different areas in the California Current System (see Daan 1980 and MacCall 1984).

A similar pattern has been recently observed for adult anchovy and sardine along the western coast of South América (Sharp, MS). Since the decline in abundance of the Peruvian anchoveta there has been no change in the overall latitudinal distribution of the fish (but see Figure 14). However, the population has receded into local refuges at major upwelling centers, where most reproductive activity takes place. These subcenters appear to be spatially isolated at low abundance years while the distribution seems to be continuous at high biomass levels. The distribution of adult sardines, on the other hand, extended shoreward in Perú and Ecuador, and then expanded northward into Ecuador and southward some 600 nm to Chile. These changes took place at a time when the sardine population was increasing and the anchoveta was receding into its subcenters.

In summary, the sardine population seems to contract its range along a latitudinal gradient, while the anchoveta appears to reduce the total area occupied by receding into isolated reproductive centers, although maintaining the same latitudinal range.

Evidence in other Clupeoid Populations

Many of these patterns of expansion and contraction have been detected in other clupeoid populations during periods of increasing or decreasing abundance. Murphy (1977), after reviewing some population dynamics clupeoid case histories concludes that the contraction of feeding and spawning range as the population is reduced "entrails the seeds of ultimate disaster" as the fishing fleet, as we have seen, usually also contracts its area of operations to maintain economic viability. This pattern results in CPUE changing much more slowly than abundance or even moving in the opposite direction. At the same time, contraction of the stock and of

the fishing fleet may lead to increasing fishing mortality. This is one of the reasons why CPUE is not a good index of abundance for small pelagic species. Additional examples of probably density dependent habitat selection in clupeoids include the Japanese sardine (Kondo 1980), the North Sea herring (ICES 1970), the South African pilchard (Crawford *et al* 1980) and the Atlantic menhaden (Schaff and Huntsman 1972). Daan (1980) provides a review of replacement case histories, phenomenon that -as we have seen- may be related to patterns of expansion and contraction.

III SPATIAL STRUCTURE

CLINAL VARIATION IN GROWTH AND MORTALITY RATES

One of the characteristics of spatial structure observed more frequently is geographic trends in growth rates and age distribution. These clinal variations in traits such as size and age have been studied mostly from the point of view of taxonomy and evolutionary ecology, in particular in relation to the issue of rate of gene flow and the differentiation of local populations.

Until 1920, ecology had been pursued as if hereditary variation within the species did not exist. This situation prevailed until the work by Turesson (1922), who coined the word ecotype when he began to look at adaptations of plants to local conditions; ecotype describes genetic variation within a single species. The term cline has been sometimes used as synonym with ecotype, but in the ecological literature it is applied in a broader way to refer to both genetic and phenotypic trends in characteristics (e.g. size, age, weight, color) of individuals in single species populations, usually along an environmental gradient. This trend is commonly associated with more or less geographically isolated segments of a population. Usually this gradient of characteristics is closely related to a gradient of the environment, such as temperature. The phenomenon is well studied in plants which grow taller in the lowlands and smaller in the mountain tops, along a gradient of altitude and temperature. Transplants and uniform condition growth experiments have generally showed that these characteristics have partly a genetic basis, as they are retained over several generations when the plants are grown under identical conditions.

These experiments have demonstrated that genetic and physiological uniformity cannot be assumed throughout the range of a species, and sometimes not even throughout the range of a single population.

Differences in morphology and physiology throughout the range can be therefore completely dependent upon genetic structure; alternatively, they can be completely phenotypic, driven by the environment (e.g. temperature); or they can result from a combination of both factors. Transplant experiments have determined that this latter possibility is the most common.

The genetic differences between ecotypes are the result of evolutionary differentiation within species subject to habitat constraints. Therefore, the regional differences are undoubtedly adaptive, because they broaden the ecological tolerance range of the population by dividing it into smaller subpopulations (demes) each differently adapted to local environmental conditions. The main problem in studies of regional variation and evolutionary ecology is the amount of genetic mixing among these demes.

Many of these topics have been studied in detail in plant populations and to some extent in terrestrial animals and sessile marine organisms, but they are seldom studied in free swimming marine species whose populations are usually assumed to mix thoroughly by virtue of active movement and advection and transport events. One exception to this situation is the use of meristic and morphometric counts as a criteria for separating different stocks of fish species. These characteristics sometimes show clinal variation, usually related to temperature gradients. Examples of these are McHugh (1951) and Vrooman *et al* (1981) for the northern anchovy; and Jordan (1963), Brandhurst *et al* (1965) and Tsukayama (1966), for the Peruvian anchoveta. Figure 20 (Margalef, 1974) shows an example on the number of vertebrae in the Canary Current Pilchard. The adaptive significance of these morphometric characteristics and meristic counts remains obscure, although such geographically variable phenotypic traits are frequently developmentally flexible and respond, as was indicated before, more or less directly to temperature (Pianka 1974).

Clinal Variation in the Northern Anchovy : Size and Age Distributions

Meristic and morphometric counts (McHugh 1951) and recently electrophoretic

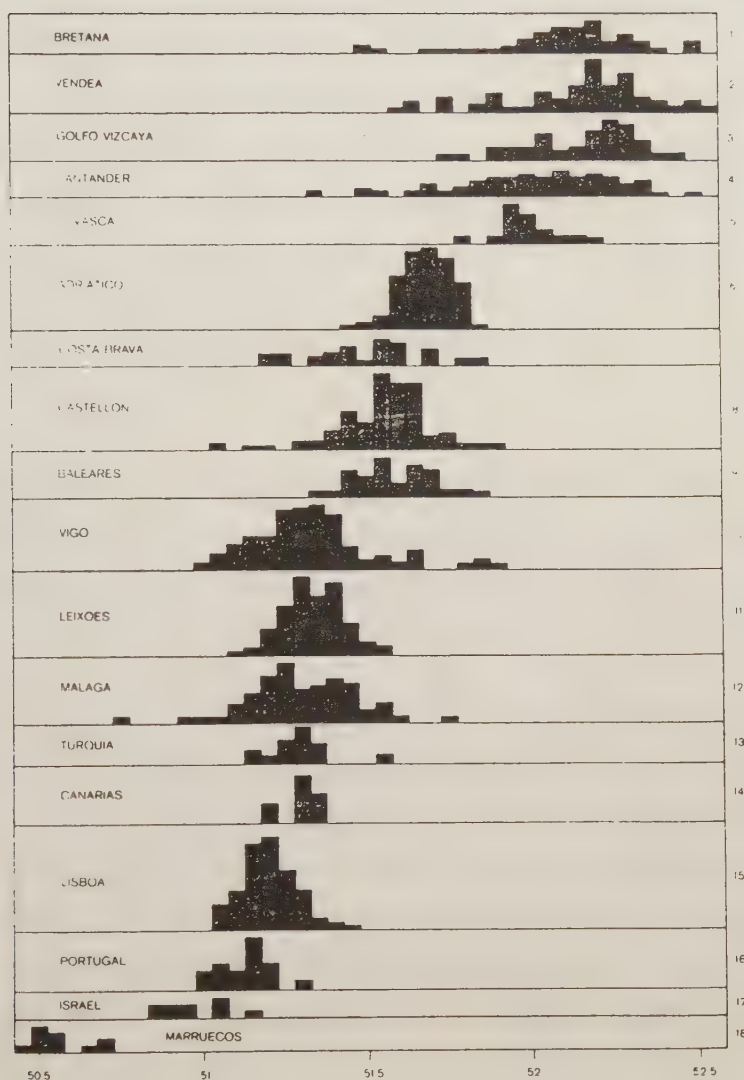


Figure 20. The average number of vertebrae in the sardine (*Sardina pilchardus*) as a function of temperature. Samples from warm places tend to have less vertebrae than fish taken in the north, colder regions. From Margalef (1986).

analysis (Vrooman et al 1981) have indicated the existence of three more or less isolated subpopulations of the northern anchovy : northern, ranging from British Columbia to approximately San Francisco; central, ranging from San Francisco to approximately Cape San Quintin in Baja California, and southern, from the Cape San Quintin area to the southern tip of the Baja Peninsula. Tagging experiments have shown that the anchovies move both directions between Central California and Southern California; they also move from Southern California to Northern Baja California. In addition it has been suggested that there is a northerly movement during the summer and a southerly movement in winter (Haugen et al 1969). Regional differences in size and age distribution have also been studied by Spratt (1975), Mallicoate and Parrish (1981), Parrish et al (1985) and Gallardo-Cabello (1985a and 1985b).

These studies suggest the possibility of incomplete mixing within the anchovy population, with one of the postulated consequences being regional differences in growth and age distribution. What follows is a brief review of these investigations and of some of the relevant conclusions advanced.

Parrish et al (1985) divided the area of anchovy distribution according to the number of samples and to the distribution of natural basins. The general region studied include Central California, inshore and offshore Southern California and Northern, Central and Southern Baja California (Figure 21). Mean length, standard deviation of length, length range and number of observations by age and month were calculated within these areas, and with this information growth and age composition were estimated. Data from 101 hydroacoustic cruises conducted from 1966 to 1983 were utilized. Their results show that there is an alongshore clinal variation in mean length at age. Fish tend to be larger in the north and smaller in the south of the range, and this pattern persists over years and includes all ages. Juvenile growth is highly variable, and the average size of individuals aged 1 1/2 years is higher in Central California (123.6 mm) than in Southern Baja California (91.8 mm), with intermediate places having intermediate values. In addition, it seems that a cross-shore gradient also exists, as fish of age 1 1/2 years are larger in the offshore Southern California region (120.0 mm) than in the inshore Southern California area (113.4 mm), see Figure 22. Interestingly, adult growth is less variable, with only minor differences among regions (growth rate for the whole area is between 6 and

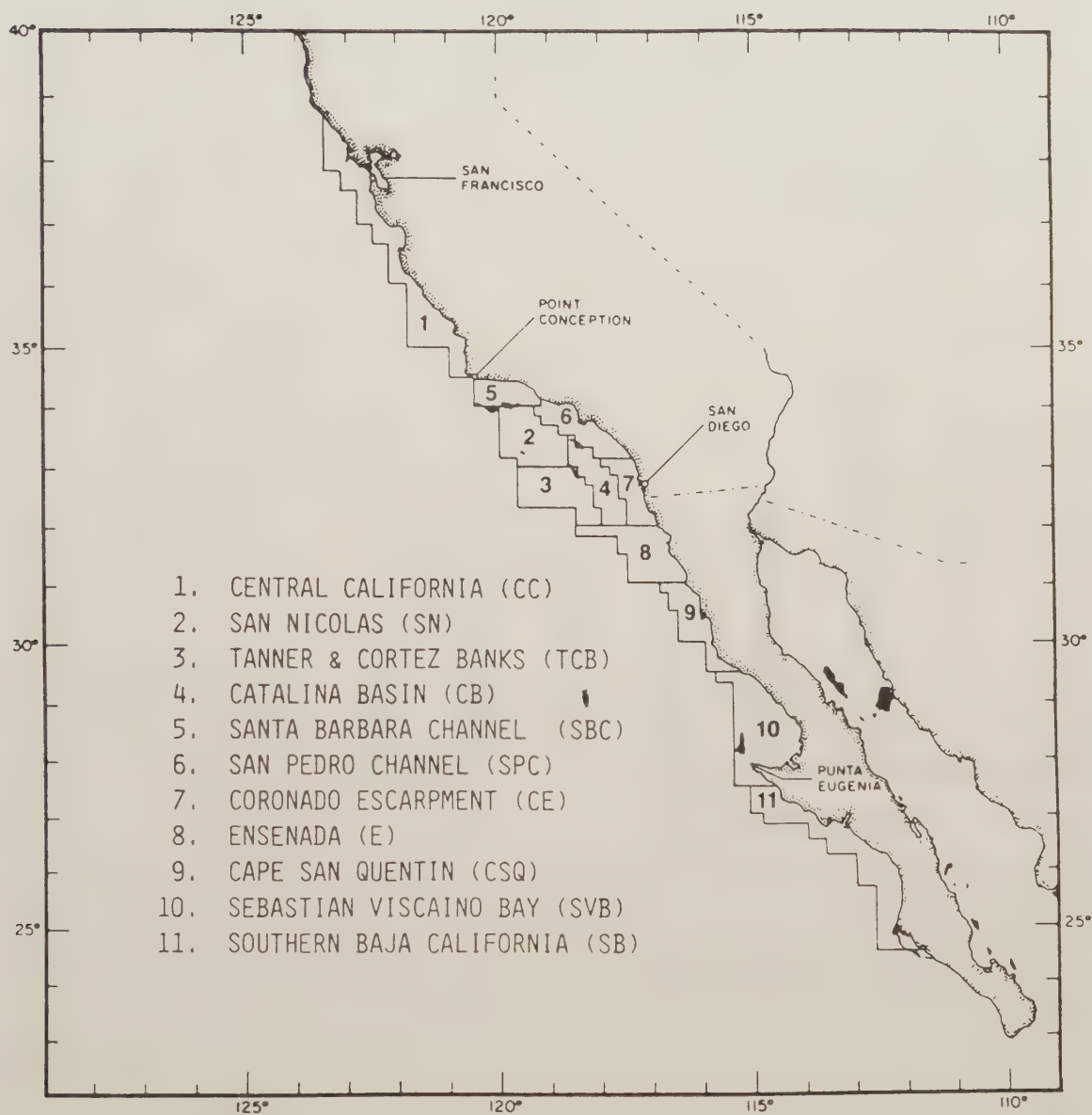


Figure 21. Geographical regions used by Parrish *et al* (1985) in their study of the northern anchovy. See Figures 22 and 23. From Parrish *et al* (1985).

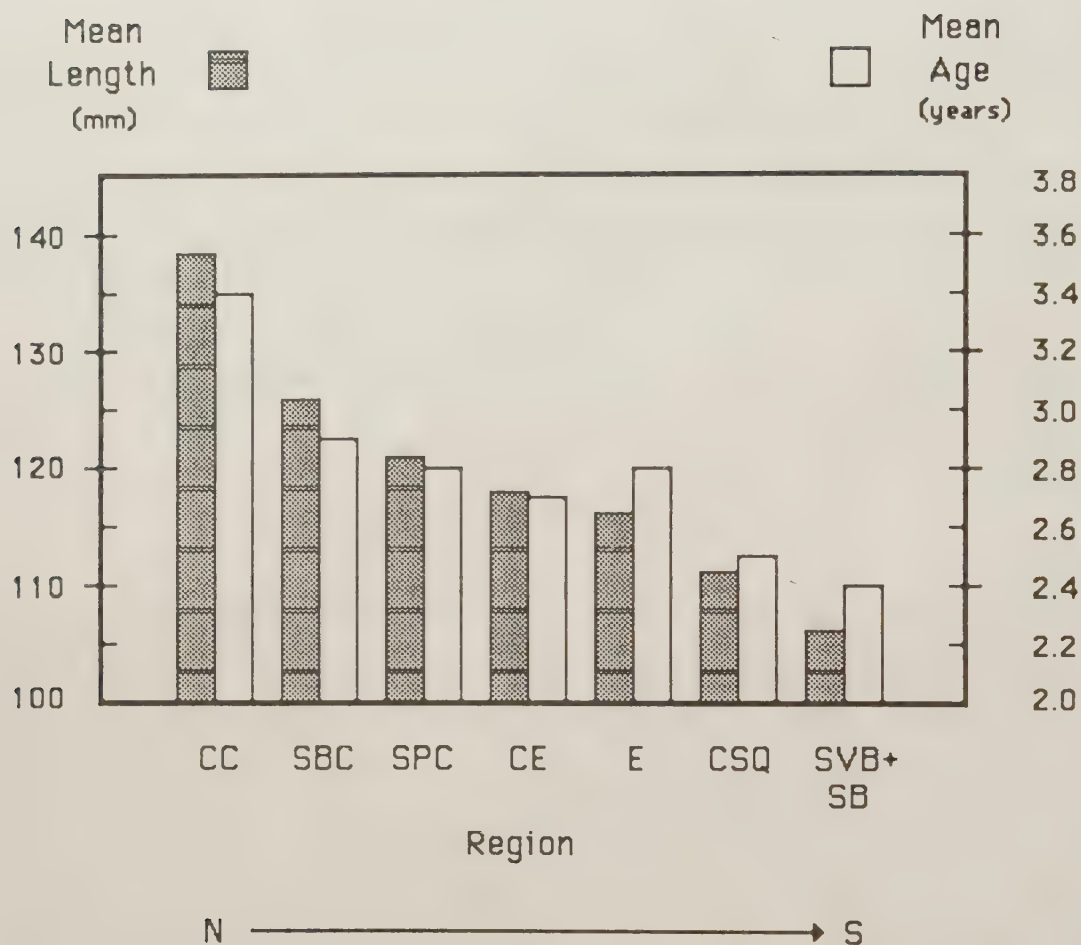


Figure 22. Mean length and mean age of adult anchovy. The alongshore gradient (north - south) is shown. Anchovy tend to be younger and smaller in the southern areas. CC = central California; SBC = Santa Barbara Channel; SPC = San Pedro Channel; CE = Coronado Escarpment; E = Ensenada; CSQ = Cape San Quintin; SVB = Sebastian Vizcaino Bay; SB = southern Baja California. There is also a cross-shore gradient, as individuals are older and larger in the offshore areas. Mean age values are 2.7, 3.1, and 3.2 years for CE, Catalina Basin and Tanner and Cortes Banks, while mean length values (mm) are 118.7, 126.7 and 130.8 for the same regions. See Figure 21 for geographical location. Data from Parrish *et al* (1985).

8 mm per year), except in Southern Baja California, where growth essentially ceases after 1 1/2 years of age.

The same alongshore and cross-shore patterns can be observed for age composition (see Figure 23 and mean age in Figure 22). Age composition by area agrees in general with length distributions. Central California is dominated by fish 3 years of age and older, while southern California has mostly 1 and 2 year olds with 0 and 3 year old individuals are less abundant. Baja California is dominated by young fish, 0 and 1 year old individuals are most common, and a decrease in abundance with increased age can be readily noticed. The cross-shore pattern is also clear, as offshore Southern California and Central California have similar age composition, with 3 year old fish dominating the samples. The San Pedro fishery age distribution has fewer 0 and 1 year old fish when compared to the age distribution from the acoustic surveys, but since young individuals tend to accumulate in the nearshore area, this difference is probably due to the closing of this region to reduction fishing. The age data from the Mexican fishery, which has no harvest restrictions, shows the same composition as that of the acoustic data.

Mais (1974) found similar patterns : he showed that the southern stock anchovies were smaller at age than individuals from the central stock, and that within the central subpopulation offshore anchovies tended to be larger and older when compared to inshore individuals. He also found that anchovies caught in Central California were larger on the average than those caught in Southern California. Mallicoate and Parrish (1981), using data from the San Pedro and Monterey anchovy fisheries showed that landings in Central California were composed mainly by large, old and heavy individuals while those in Southern California were predominately composed of smaller, younger individuals.

Thus, anchovies grow initially faster and are larger and older in the northern and offshore areas of the distribution; they are smaller and younger in the southern and inshore regions of the spatial range. This is probably a consequence of alongshore and cross-shore clines in both age and size at age.

Some of these patterns are clear even over a smaller area. The landings of the Ensenada based Mexican fishery show the same age and length distribution

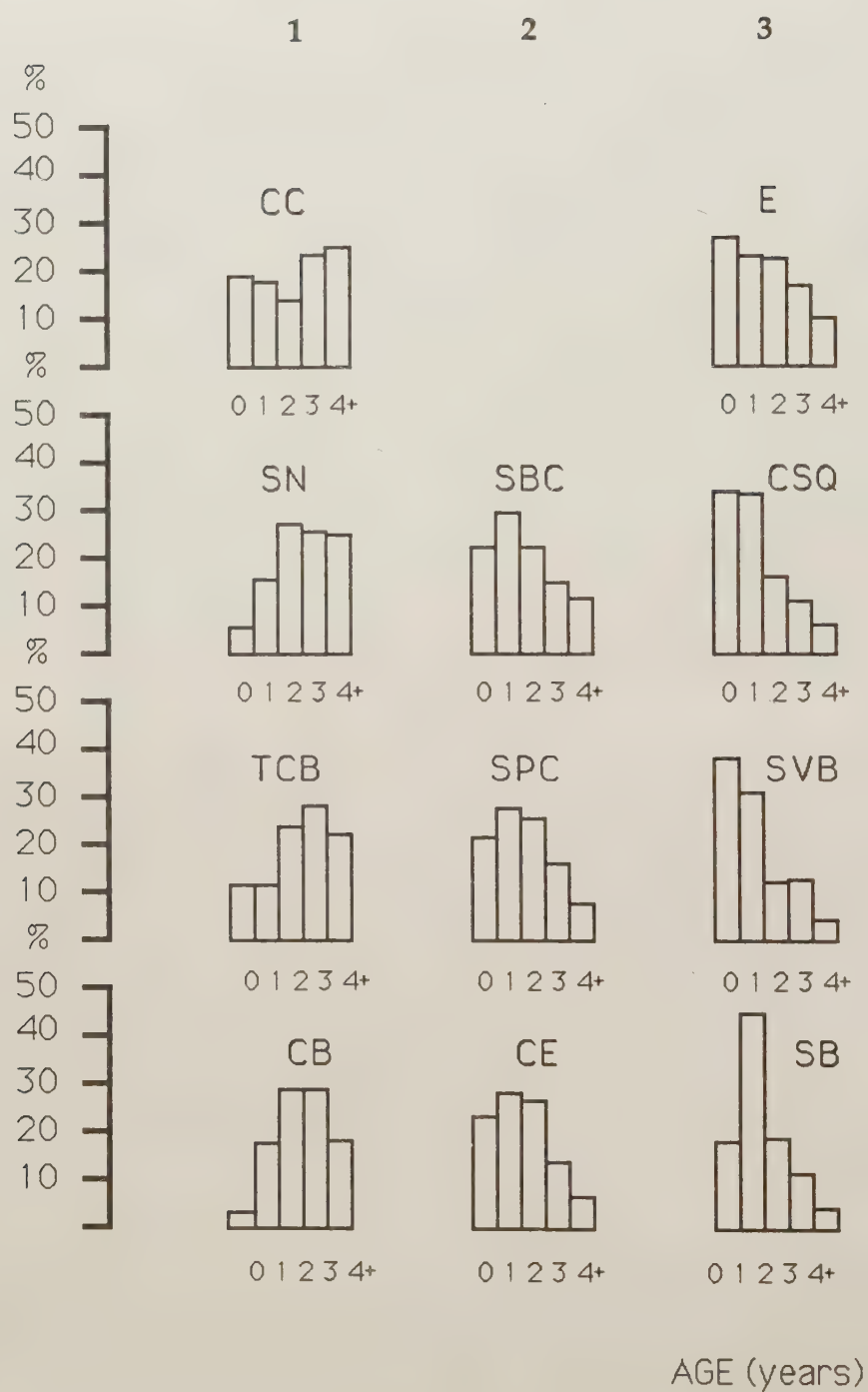


Figure 23. Northern anchovy age distribution by region. 1. Central California and offshore areas of the Southern California Bight; 2. Inshore areas of the Southern California Bight; 3. Baja California. See Figure 21 for area codes. Data from Parrish *et al* (1985).

patterns, with large, old individuals usually in the northern fishing grounds (north of Ensenada) and small, young individuals in the southern fishing areas (Cape San Quintin region) (pers. comm. Tom Barnes, Living Marine Resources, San Diego). Gallardo-Cabello (1985a, 1985b) distinguished two different subunits in the Ensenada area, according to meristic and morphometric characteristics. He used Mexican data collected by the Zapata Fishing Company and found that in the northern subunit growth rate is higher and the landings tend to be dominated by older individuals while in the southern subunit fish are in general younger and smaller.

However, as Parrish et al (1985) indicate, the interpretation of these results depends heavily in the structure of the population in the area of study. Also, some of these patterns could be the result of size dependent migration. For example, Parrish (1983) has proposed the existence of a fall spawning stock inhabiting Central California and the offshore region of Southern California. In addition, the central and southern anchovy subpopulations mix to an unknown but seasonally varying degree in the Cape San Quintin area in Baja California (Vrooman et al 1981, Parrish et al 1985). Both of these conditions could possibly affect regional age and size distributions.

Therefore, the most general conclusion from the studies is that If most of the fish in the area are from the central subpopulation, then the mixing of individuals is not complete, otherwise length distribution and age composition would be the same everywhere. However, the patterns also seem to indicate that distributions are strongly related to the gyral circulation within the Southern California Bight. In general, anchovies appear to be concentrated in areas where the prevailing currents will transport eggs and young larvae to the inshore area, where environmental conditions are presumably better for them. Juveniles will then tend to be advected North and offshore where feeding conditions are more adequate for rapid growth (Parrish et al 1981). This movement (advection and/or migration) may be influencing the local demographic structure (Margalef 1986) because in areas where transport or movement are strong the age distribution will reveal an apparent higher mortality of young individuals. This could explain the relative abundance of young individuals in the inshore areas, and the apparent lack of old fish. On the other hand, older individuals tend to accumulate in peripheral areas, with a consequent reduction in apparent adult mortality rates (Figure 24). This could also help explain

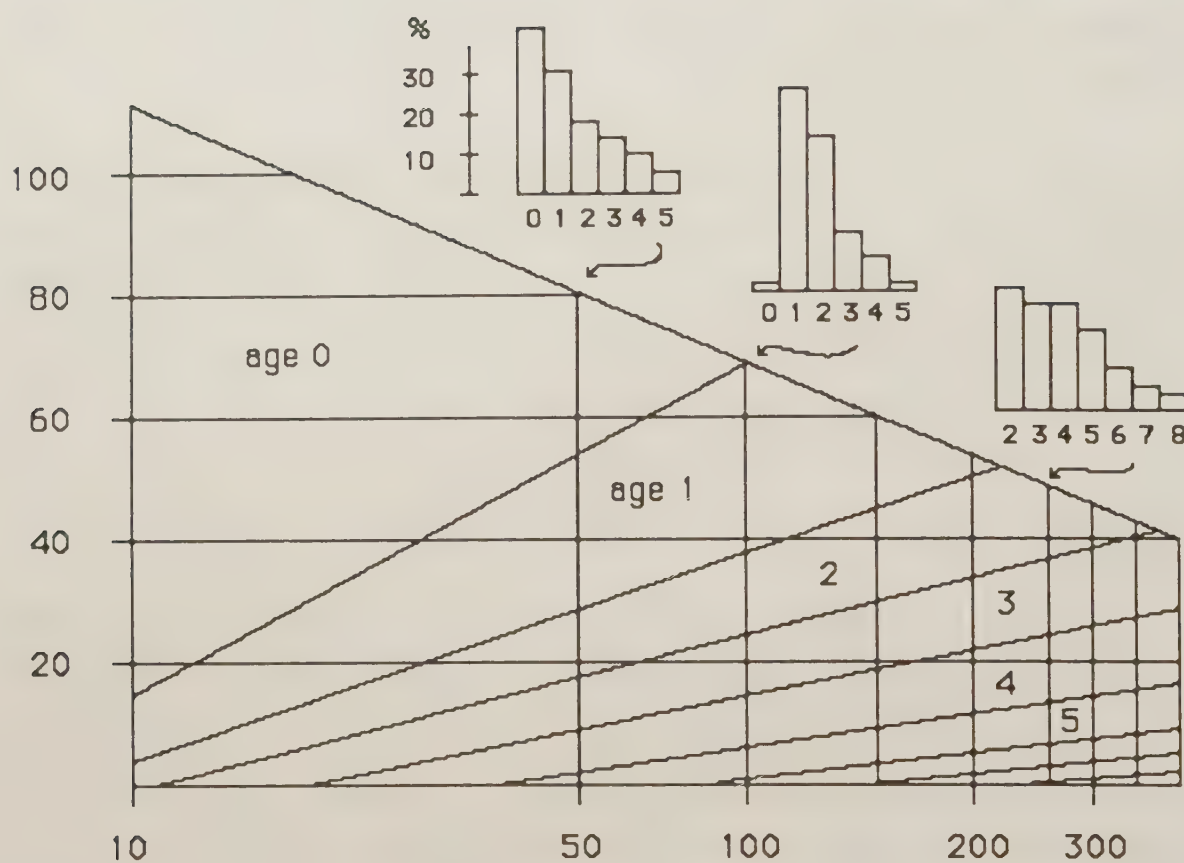


Figure 24. Theoretical age structure of a population as a function of distance from the reproductive area. Both the density of the population and the relative proportion of younger age classes diminishes with increased distance from the reproductive center. Redrawn from Margalef (1986).

why the nearshore, recruitment areas contain relatively more young individuals (see Figure 23) and the offshore, peripheral areas tend to have a large proportion of old individuals, but no apparent recruitment.

Thus the active movement, the probable existence of a fall spawning stock and the relative mixing of central and southern subpopulations all play an important role in the intrapopulation mixing in the northern anchovy. However, despite the problems regarding the interpretation of results, it is clear that the age and size distributions are not homogeneous within the range of the population, not even over a small area such as the Ensenada region. Therefore, the structural homogeneity of the population should be viewed with caution, even in the local habitat, or else the definition of locality should be geographically very restricted. It is highly likely that corresponding clinal patterns would be found in the Pacific sardine and the Peruvian anchoveta, given the similarities of these and other clupeoid populations to the northern anchovy.

IV FINAL CONSIDERATIONS

As we have seen, DDHS in the form of Expansion and Contraction of ranges seems to be a fairly common trait in clupeoid populations. The Pacific sardine, northern anchovy and Peruvian anchoveta examples show that changes in area occupied may be compounded by the extra added mortality due to fishing; also, the behavior seems to be affected by environmental changes which may trigger the cycle by limiting reproduction and finally, biotic interactions may play a major role in distribution, in particular interspecific competition at the borders of the range.

The examples (in particular the northern anchovy) show that, in general there is a more or less permanent center of distribution, although what can be considered average conditions for any of the populations is a far more rare than common event. For the California sardine and the Peruvian anchoveta, there seem to be isolated centers (demes), to some extent independent of each other, which can be considered secondary centers of expansion when the population increases. Thus, the Ideal Free Distribution may also operate at the local scale. This produces a seemingly continu-

ous distribution at high density and a separation of subunits at low abundance.

Both location and density of marginal areas are highly variable. An exception may be the offshore area where transport and advection restrict the distribution, and the clear boundaries set by physical factors such as temperature and oxygen.

The patterns associated with clinal variation in northern anchovy are more evident. It is clear that there is an accumulation of older individuals in the offshore areas of the SCB. Also, there is a tendency for individuals to be larger and older in the northern end of the distribution, and to be smaller and younger in the southern limits of the range. A conclusive interpretation depends on the extent of mixing between the central and southern subpopulations and the possible fall spawning stock. However, the data shows that the distribution of size and age is not homogeneous.

It is difficult to evaluate to what extent the clinal variation is affected by the expansion and contraction process. In order to do this, an analysis of size and age distributions for periods of high and low abundance would be necessary.

IFD assumes that most individuals are identical, differing only in its choice of habitat. However, this choice may be influenced by size, age and physiological status (i.e. feeding condition and timing of spawning) as well. Thus, if a part of the population matures faster, it could presumably secure the central places before the rest of the stock. This proposition was explored by Levedeb (1969) with his Theory on Elementary Populations. Following a somewhat similar idea, Mathisen (1979) proposed that the Peruvian anchoveta population is composed of isolated centers differing in physiological state (i.e. time of spawning). In clupeoids, habitat selection is further complicated by the fact that this species are obligated schoolers. At extreme low densities, most of the population may be composed of a few isolated schools. Size of school appears to be genetically determined for many species, although the mechanism that relates schooling behavior to density dependent responses is not clear.

The effect of fishing could be directional in such a population, because those spawners that take the central place experience the higher fishing mortality rate, as the fishing ports are usually closer to the distribution central areas. Thus in the case of heavy fishing, this part of the population will be the first to disappear, together with its genetic component. Those individuals living in the peripheral areas (which

presumably are not as well adapted as the central individuals) will then move to the more favorable regions in the center where density is now lower. This part of the population will also be heavily fished. The end result of such a process is that the remaining population will be genetically made up mostly by peripheral individuals, which although help in keeping diversity in an unfished population, are not well adapted to the most prevalent conditions, because they did not form part of the bulk of the spawning biomass. This “weak” gene pool will increase then at a lower rate, decreasing the probability of recovery of the population.

Therefore, fishing is a directional force selecting against those individuals that form the spawning peak. The remaining phenotypic distribution will be richer in individuals that were formerly at the tail ends. The key assumptions here are that the population mixing is not complete (high viscosity case of MacCall, 1984); and that there is a delay in tracking the environment, so that the population fails to assess the decreased (due to fishing) quality of the central habitat over the short period.

On the other hand, the peripheral groups are most likely to suffer the consequences of the environmental and biotic (mostly interspecific) interactions. It is therefore probable that during a contraction process these groups will be the first to disappear, particularly if the population center is fixed in space. Under these conditions, marginal areas experience the large fluctuations. However, the Pacific sardine pattern was different because the northern segment of the population collapsed first, shifting the center of distribution to the south. It is likely that the population was composed of relatively isolated groups, responding independently due to low mixing. The intensity of the response depended on the strength of the northward/southward migration that was probably size dependent. The southern end of the cline was not affected until the fishing fleet concentrated in the SCB due to the collapse of the northern segment, and the southern groups were not able to withstand the added fishing mortality.

It is likely that density patterns are similar to those described by Brown (1984). In general, it seems that density is higher at the center of the distribution and falls off symmetrically with distance, following a normal curve; environmental variation will tend to truncate this distribution, typically at only one end of the range (but see Rapaport, 1982 for some examples in which density is higher in the periphery, due to density dependent effects in the center).

Assuming IFD, and if the distribution is relatively normal and the center is

approximately fixed, the marginal areas could be used as indicators of abundance. These areas can be sampled with a low effort and could yield a fast way of learning when the population has passed certain level, either decreasing or increasing. If the population has reached the marginal areas during an expansion cycle it means that the central region is already occupied, and a certain size has been exceeded. The opposite is true during a contraction process.

Since most clupeoid species are obligated schoolers, total area occupied and schooling behavior is another characteristic that can also be used as indicator of, or related to the condition of the population. This idea has been put forward by Sharp (1981) who considers that the area occupied and the aggregation of schools are among the best indicators of the condition of small, pelagic fish populations. Csirke (1980) has shown a relation between the adult anchoveta distribution area and density dependent recruitment, and MacCall (1981) has proposed a model based on cannibalism as one of the density dependent underlying mechanisms in anchovy recruitment.

This review has been made with the purpose of describing patterns behind certain aspects of population heterogeneity. As we have seen, these characteristics are important enough to warrant their consideration when assessing and managing fish populations. Therefore, this information on the behavioral characteristics of some clupeoid populations may lead to the identification of critical factors, much needed to develop better evaluation techniques.

CHAPTER II HETEROGENEITY OF THE NORTHERN ANCHOVY FISHERY

I INTRODUCTION

One of the basic assumptions in classic fisheries models (e.g. Baranov 1918) is that of homogeneity of fishing activities over space. This assumption is at the center of most models used for fisheries management, which fall into two categories: the dynamic pool models (e.g. Beverton and Holt 1957, Ricker 1975) and surplus production models derived from the logistic equation or some extension of it (e.g. Schaefer 1957, Pella and Tomlinson 1969). Both approaches deal with a unit stock of fish defined as a closed (no interaction with the exterior), self sustaining group of individuals in which fishing mortality is proportional to fishing effort. There are two critical statements in this definition: The assumption of a stock as a closed, self sustaining unit; and the proportionality of fishing mortality and fishing effort. This latter condition is only met if the fishing effort is uniformly distributed over a constant area.

The actual space-time utilization patterns of a fishing fleet are however highly variable; but despite their importance, they have not been systematically studied. Frequently, fishing effort is heterogeneous both in space and time and the uniformity condition is very seldom fulfilled. Some recent research on this topic can be found in Hillborn and Ledbetter (1979), Caddy (1984), Millington (1984) and Hillborn (1985a and 1985b). The last author has identified four components of the dynamic behavior of a fishing fleet: a) investment/disinvestment, which includes "birth", aging and "death" of fishing vessels; b) movement, which looks at the basics of effort allocation: when, where and what to fish for; c) catching power and harvesting efficiencies as influenced by competition and learning; and d) discarding, or the choice of what to keep and what to let go. This chapter is concerned with the second component of fleet dynamics, in particular with the problems associated with the choice of fishing locations: the basic when and where to fish decisions faced by any fishermen.

This chapter addresses therefore the fishery heterogeneity problem by means of describing some of the movement patterns of the fleet and aerial fish spotters harvesting the northern anchovy subpopulation. The particular set of problems

reviewed are those related to the choice of fishing areas; when and where to fish in order to harvest efficiently. The anchovy fishery is spatially constrained to the coastal areas and this regionality will be studied in both the U.S. and Mexican fleet by looking at the effort and harvest space utilization patterns. Also of interest will be the description of concentration rings (e.g. distance decay patterns) around the main fishing ports. Additionally, a description of the mean distance the vessels travel to fish and a study of its relation to several biological and economical variables will be performed using a factor analysis technique.

SOURCES OF INFORMATION

Aerial Marine Resources Monitoring System (AMRMS)

Since 1962 the NMFS (National Marine Fisheries Service), SWFC (Southwest Fisheries Center) has contracted with a selected group of pilots to fill out logs of their observations while locating fish for commercial fishermen. This program has been described by Squire (1972) and Caruso *et al.*, (1983). During the first year the spotters recorded their observations on tape recorders, and these tapes were later transcribed by NMFS personnel. Due to some problems with the transcription, the next year a system of flight logs was instituted with the pilots completing the logs themselves. These first logs were simple, depicting the coast and island outlines, and the pilots recorded their flight path and sightings freely. In 1968 the second generation of flight logs was brought into use, with the addition of a grid system based on 10 min grid squares, which represent about 8 miles by 10 miles at the latitude of Southern California.

The fish species more commonly observed by the commercial fish spotters while operating off central and southern California, and northern Baja California, México are the northern anchovy, *Engraulis mordax*; jack mackerel, *Trachurus symmetricus*; Pacific bonito, *Sarda chiliensis*; Pacific mackerel, *Scomber japonicus*; Pacific sardine, *Sardinops sagax caerulea*; and bluefin tuna, *Thunnus thynnus*. Other species such as Pacific barracuda, *Sphyraena argentea*; yellowtail, *Seriola lalandei*; white seabass, *Atractoscion nobilis*; and albacore, *Thunnus alalunga*, are observed by the pilots and are sometimes caught by the commercial fleet with the aid of aerial spotters. Other

species of fish, as well as marine mammals (whales and porpoise) and invertebrates (squid) have been observed and recorded (Squire 1983).

The pilots normally fly out of Santa Barbara, Los Angeles and San Diego areas. They survey a region that extends from Half Moon Bay to Cedros Island (off Baja California, México) and as far offshore as Tanner and Cortez Banks. The majority of flights, however, are concentrated in the southern California Bight, extending from Point Conception to Ensenada, Baja California, where the purse seine fleet expends the longer part of its effort.

In 1977, two data bases were developed and later modified (see Caruso *et al* ,1983) to systematize information and to facilitate research and the calculation of an anchovy abundance index. The first data base contains the effort information, effort being defined as the number of ocean blocks over which a pilot passes. The effort data base contains the approximate flight path in consecutive blocks flown by each pilot for each flight. The second data base contains the sighting information, a sighting being defined as a drawn circle describing the limits of a school or school groups of fish or groups of mammals on a pilot's flight log. An effort record contains the year, month, day, pilot, flight, time, plane and block numbers for all blocks covered in that flight. The sighting data base contains the first seven elements as the effort records (year, month, day, pilot, flight, time and plane) and, in addition, the block number where the sighting occurred, species code and tonnage information. Most of the flight observation effort south of the United States - México border has been offshore in search of bluefin tuna and, as a result, nearshore areas commonly having schools of anchovies are rarely surveyed and such schools are therefore not reported.

The data from pilot observation logs are used to calculate an annual index of abundance for the most important species, particularly anchovy. Squire (1972),defined a larger region wherein all blocks were pooled, and combined these regions to produce an overall index of apparent abundance. Day observations are processed separately from night observations and provide separate indices of abundance, which are estimates of observable biomass per unit area.

Since observability of anchovies varies with time and season, short term aerial observations are of limited utility for the calculation of overall abundance (PFMC, 1984), but when averaged over a long period (usually a year), the information provides an index of relative abundance. This index is available from 1962 through 1978.

No systematic aerial survey for anchovy has been attempted on a regular basis, although much of the methodology exists. For example, Cram (1977) reviews an extensive systematic aerial/acoustic monitoring program that has been developed in Southwest Africa.

Fisheries Monitoring Records

During 1965, the California Department of Fish and Game (CDFG) started a system of trip logs required of all boat operators that land anchovies for reduction. The format of these logs has changed several times, but they have consistently provided information on catch, area and time away from port. Logs for unsuccessful trips are not necessarily reported.

In 1980, Doyle Hanan (CDFG, pers. comm.) examined logs from a sample of seven typical vessels most of which were active from 1969 to 1979, creating the data base which is the source of information for this study. This base contains two types of records: trip and set. The trip record includes information on leaving, returning and scouting dates and times, log number, vessel number, captain code, gear type, pounds for reduction and number of sets. The set record includes starting and ending set date and time, species code, estimated tons captured, use of plane and sonar, block number where the set was made and scouting time. The blocks are the same as those used by the spotter planes, on a grid of 10 by 10 min. squares, corresponding to approximately 10 miles by 8 miles at the latitude of Southern California.

The objective in Hanan's study was to develop some measures of catch per unit of effort (CPUE) adequate to describe changes in abundance. He therefore developed two measures of CPUE: catch per day and catch per hour, and found that catch per day has been rather constant over a wide range of fish abundance and availability, and that catch per hour appears to be more sensitive to availability and varies greatly from semester to semester.

One important factor that complicates the interpretation of these results is the limited vessel hold capacity and reduction processing capacity. Because of limited reduction capacity, processors often impose landing limits on the vessel which are

generally less than vessel capacity, so that a vessel can catch its limit in one or two sets. Aerial fish spotters scout for commercial concentrations of fish, and in many cases direct the setting of the net thereby increasing success rate and decreasing vessel scouting time. Therefore, both catch per trip and catch per hour may reflect vessel or reduction capacity more than stock abundance. (PFMC, 1984).

Zapata Fishing Company Data

The Ensenada-based Pesquera Zapata Company, which processes about 80% of all the Mexican catch of anchovy, established during 1977 a vessel set log system for all of its anchovy seiners. Area of fishing, number of sets, catch per set and water temperature are recorded daily by each vessel. During 1978, the Zapata Company in conjunction with Living Marine Resources, a San Diego-based consulting firm in marine resources developed and implemented an industry research program on northern anchovy. This program included the set log system as well as a parallel survey (initiated in June 1978) designed to obtain biological information. When fish are available, about one kilogram is sampled from the catch before the fish are unloaded. An attempt is made to obtain samples from each of the major zones of operation. At the Zapata laboratory, all fish are measured and a subsample of 20 fish is selected from each sample, weighed, examined for degree of maturity, and the otoliths are removed for aging. The otoliths are aged using California Department of Fish and Game methodology.

The biological information has been coded and divided into three different files: a fishery file, a length file and a biological file. The fishery file contains information on fishing vessel, area of fishing, date of capture and landing, and total estimated tons caught. The length file contains the data on fish length for the whole sample, usually around 90 fish. The biological file contains the information on age, sex, degree of maturity, otolith condition and weight for each of the 20 fish subsampled.

II PATTERNS OF SPACE-TIME UTILIZATION : DISTRIBUTION OF EFFORT AND HARVEST

DISTRIBUTION OF AREAS AS A FUNCTION OF DISTANCE FROM THE FISHING PORT

U.S. Fishery

To describe some spatial anchovy fishing patterns on the Southern California fishing fleet, a characteristic distance was assigned to each 10' by 10' California Department of Fish and Game statistical squares. This distance was measured from San Pedro which is the base port for most of the fleet to the center of each square. When a square was not symmetrical due to the presence of islands or the coastline, a center of gravity was calculated by eye and this point was the reference for measuring its distance to port. In this way, a unique distance was assigned to each square up to 65 nm from San Pedro.

The area occupied by each block in the region was also measured, and these areas were assigned to two categories: available to exploitation, and closed to exploitation due to the anchovy fishery three-mile coastal regulatory closure (see PFMC, 1984). The squares with available area were further classified according to whether there was or was not a harvest taken by the vessels sampled during the period considered, which was spring and fall from 1969 to 1979.

The results are shown in Table 3 and Figure 25. The Table shows that a total of 89 blocks are available to the fishermen within 65 nm from San Pedro, and there was exploitation in 43 (48%) of them. The total area is 6243.2 nm² of which 89% (5559.2 nm²) is open to exploitation and 11% (684 nm²), is open only to harvest by live-bait fishermen due to regulations. Of the available area, 50.2% was harvested (2790.4 nm²) and 49.8% (2768.8 nm²) was not utilized by the reduction fleet.

In Figure 25 it can be seen that the total area in general seems to increase proportionally to the square of the distance from the fishing port; but in a somewhat

Table 3. Distribution of the area categories as a function of distance from the fishing port. Southern California anchovy fishery.

Distance (nm)		Nº blocks		Area (nm ²)				Total
Range	Midpoint	Harvested	Total	Harvested	Not Harvested	Total	Closed	
0 - 5	2.5	1	1	0	0	0	32.0	32.0
5 - 10	7.5	1	2	57.6	0	57.6	45.6	103.2
10 - 15	12.5	5	5	184.8	0	184.8	121.6	306.4
15 - 20	17.5	5	5	296.0	0	296.0	57.6	353.6
20 - 25	22.5	4	4	277.6	0	277.6	40.0	317.6
25 - 30	27.5	4	6	279.2	0	279.2	57.6	336.8
30 - 35	32.5	6	7	440.8	0	440.8	39.2	480.0
35 - 40	37.5	5	10	395.2	245.6	640.8	50.4	691.2
40 - 45	42.5	4	8	320.0	316.0	636.0	0	636.0
45 - 50	47.5	2	8	89.6	407.2	496.8	71.2	568.0
50 - 55	52.5	3	9	240.0	384.0	624.0	9.6	633.6
55 - 60	57.5	2	16	129.6	966.4	1096.0	111.2	1207.2
60 - 65	62.5	1	8	80.0	449.6	529.6	48.0	577.6
TOTAL		43	89	2790.4	2768.8	5559.2	684.0	6243.2

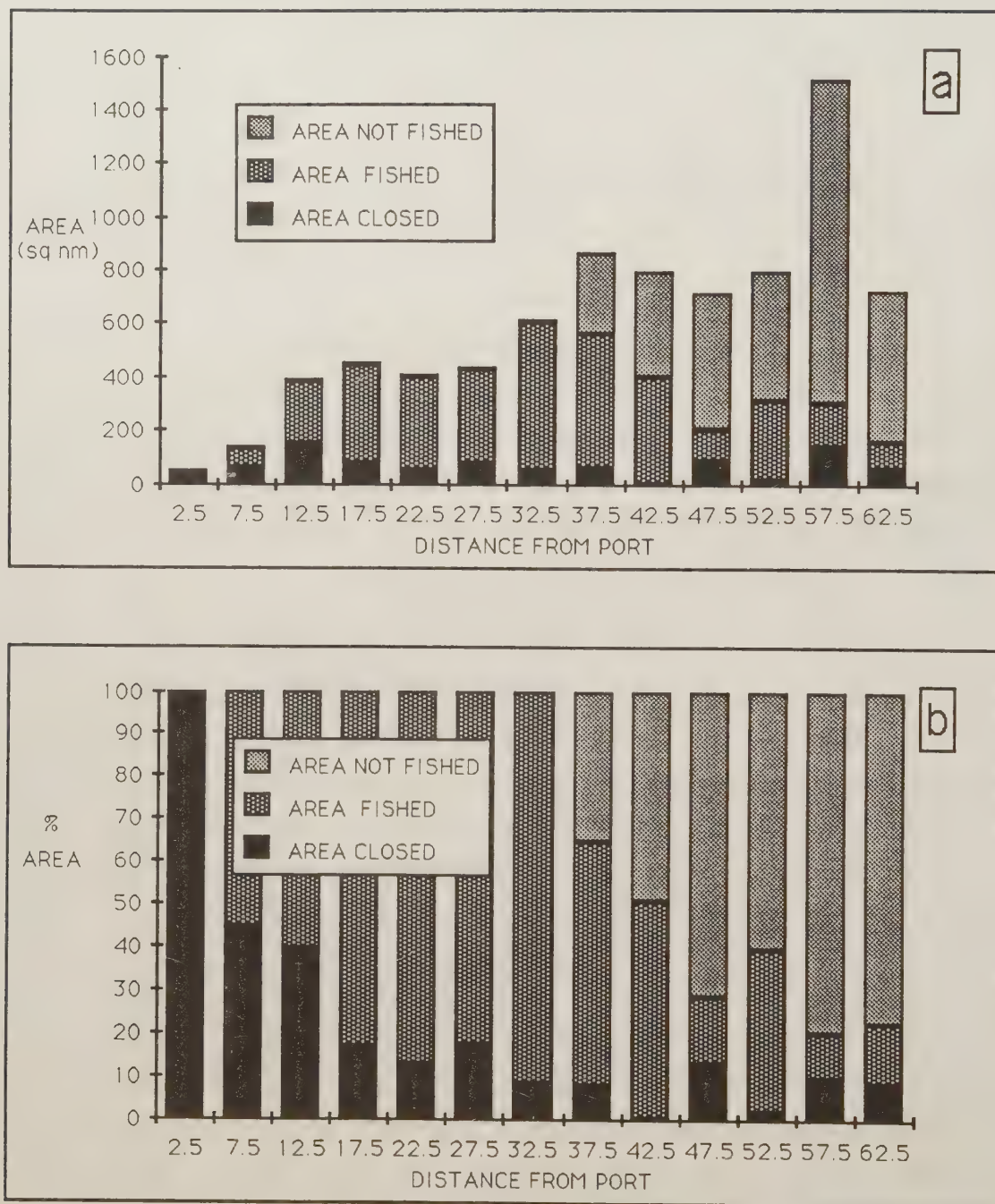


Figure 25. Distribution of areas as a function of distance from San Pedro. a) Distribution of areas; b) Relative proportion of areas. The relative proportion of the area closed decreases with distance, while the proportion of area not fished increases.

irregular fashion due to Santa Catalina and San Clemente islands. The 3-mile inshore closed area is, in absolute terms, roughly constant at all distances. The harvested area is also approximately constant up to 40 nm from port, and decreases after that. There is no available area that was not exploited within 35 nm of San Pedro, and at greater distances the unexploited area is almost constant, except at the 55-60 nm range, where in a large available area no school was taken.

The relative importance of each category at each distance stratum is also shown in Figure 25. The relative importance of the closed area is much higher near the fishing port, and decreases exponentially with distance. This relative importance is probably even higher, because the closed area is in the inshore region, where the concentration of large anchovy schools is often very high. The area harvested increases its relative importance up to 35 nm from port and then declines with distance in a somewhat exponential fashion. The unexploited area becomes dominant beyond 35 nm from San Pedro.

In summary, the San Pedro fishermen exploit 100% of the available area up to about 35 nm from the fishing port. After this distance, many squares are left unexploited and these form a large proportion of the total available area at distances greater than 35nm from port.

Mexican Fishery

To study the space utilization patterns of the Mexican anchovy fishery fleet based in Ensenada, a characteristic distance was assigned to each 5' by 5' statistical square used by the Zapata Fishing Company. The technique used to calculate distance and area occupied by each block was the same used with the U.S. data. In this way, a unique distance and area occupied was assigned to each block up to 100 nm from Ensenada.

There is no closure in the Mexican fishery, except for the prohibition to fish inside Bahía de Todos Santos (the Ensenada Bay); since most of the region is available to exploitation, there is only one area category. In addition, there are no large islands near the fishing port and the coastal shoreline follows a more or less straight NW-

SE path. Therefore, the distribution of areas available for fishing simply increases with the square of the distance from Ensenada. Within the available areas, only those within 20 nm from the coast were predominantly exploited by the Mexican fishermen. The offshore region is very seldom utilized.

U.S. FISHERY PATTERNS

Aerial Effort by Year

With the objective of describing some of the patterns of distribution of aerial effort over the whole area in a year, the AMRMS files were summarized, and three years were chosen for the general description of the aerial effort. Description of the effort devoted to all the pelagic species in a year was important, despite the fact that strong seasonal patterns were expected. The aerial effort is defined as the number of blocks over which a pilot passes in a searching flight and is therefore expressed in block-flights. It is important to notice that most of the aerial effort has been spent in Southern California waters and almost no searching effort has been devoted to Mexican waters.

The years chosen were 1966, a year with moderate anchovy abundance and low catch ; 1975, a year with high anchovy abundance and catch, and 1982 which due to the well-documented El Niño phenomenon was (from the environmental point of view) a very unusual year, with both low abundance and low catch. Table 4 and Figure 26 show some of the results of this description.

Table 4 shows that the aerial effort - both in number of flights and in number of block-flights - devoted to pelagic resources was similar during 1966 and 1975, and about 30% higher during 1982. The area surveyed was generally the same, with a slight increase in 1975. The highest number of sightings was recorded during 1966 despite the increase in effort during 1982. The spawning biomass was large in 1975 and the U.S. harvest was one of the largest ever. The year 1966 produced a very poor harvest with a moderate spawning biomass (this was the first full year in which an anchovy reduction fishery was allowed in California. Catch may have been low due

Table 4. Summary of aerial effort for all pelagic species for 1966, 1975 and 1982. The year summarized are 1966, with a moderate anchovy abundance and low catch; 1975, with high anchovy biomass and large landings, and 1982 with low abundance and low catch but high environmental variation.

Variable	1966	1975	1982
Effort (block-flights)	11509	11330	15370
Area (Nº of blocks searched)	224	280	249
Number of Flights	597	629	666
Number of Sightings (all species)	2564	1705	2196
Estimated anchovy spawning biomass (1000 tons)	972.2	3642.4	609.4
U.S. catch (1000 tons)	24.8	141.6	40.9

to non-biological reasons, such as the development of industry markets, the initial learning period for the fishermen and a complicated set of area quotas) and 1982 was a year of medium harvest and very low spawning biomass. There is a slight increment in aerial effort associated with many of the islands and banks, and it is important to notice that a few blocks (usually only 4 or 5 near the airports) get most of the attention all the years.

The maps of spatial distribution (Figure 26) show two areas of high concentration of aerial effort: one is the area around San Pedro, where the wetfish fleet spends most of its time, and the other is the area between Santa Barbara and Port Hueneme where a smaller fishing fleet based in the latter port is operating. During 1966 the aerial effort was very concentrated around the two centers, with a slightly higher activity in the northern region and the searching going on as far as Tanner and Cortéz banks, locations where jack and Pacific mackerel were sought. In 1975, the effort pattern was similar around the San Pedro area, but more intense than during 1966. The northern effort was slightly shifted to the south, perhaps because the spotters were following some other important species, and it was not as intense as it was during 1966. The patterns during 1982 were completely different: the northern area stretched along the coast and joined the southern area, which almost disappeared. The effort was centered around Port Hueneme where the anchovy fishery remained active. The San Pedro area received very sparse attention, perhaps due to the lack of interest in processing anchovy this year or perhaps due to the abnormally high temperatures that forced many species to move to the north. The aerial effort for the remaining areas was insignificant, as it was for the other two years, but extended nonetheless as far offshore as Tanner and Cortéz banks.

In summary, there are two main areas of aerial effort concentration, that reflect the location of the fishing fleets: San Pedro and Santa Barbara Channels. Also, the aerial effort is normally concentrated mostly around the San Pedro area, and a few blocks get most of the spotters' attention. However, El Niño year of 1982 was very unusual because the aerial effort almost disappeared from the San Pedro area. It is important to notice as well that there is no obvious correlation between the spatial distribution of aerial effort and years of high or low anchovy spawning biomass.

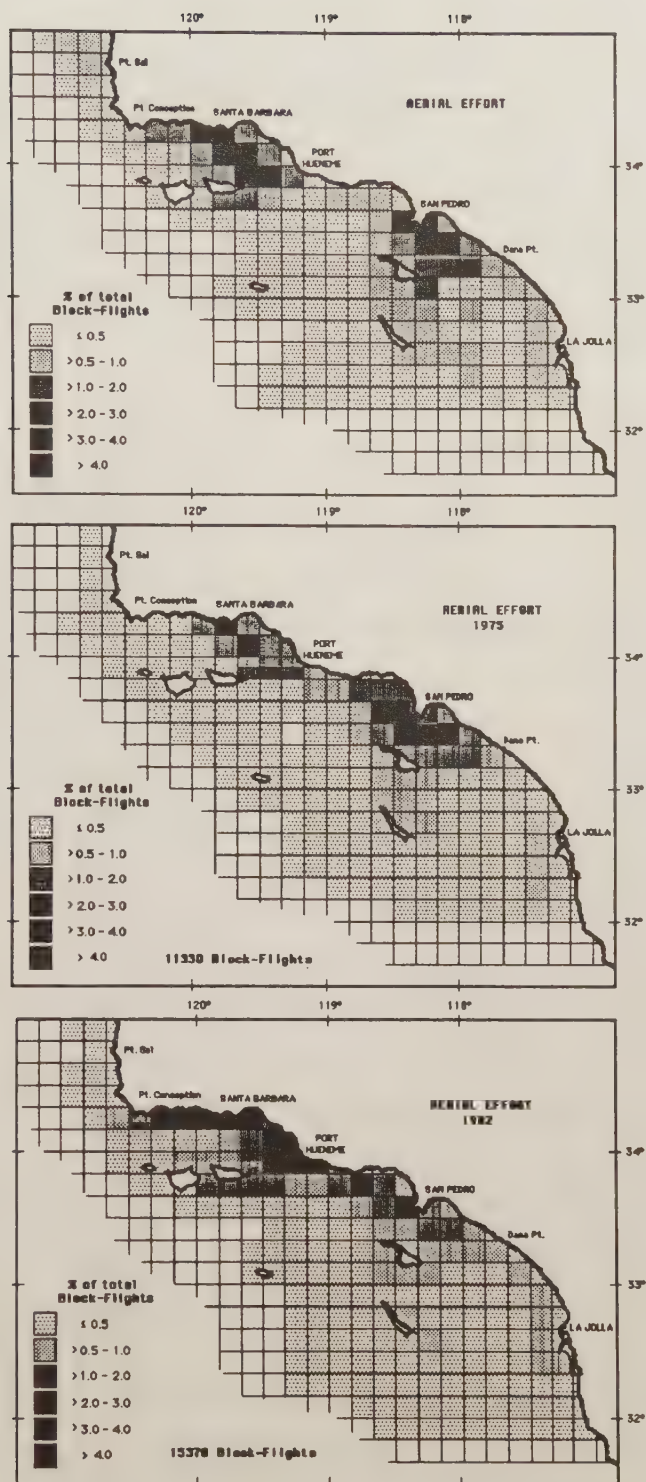


Figure 26. Aerial effort by year. Spatial distribution of aerial effort for all pelagic species in three years of varying biomass and landings.

Seasonal Variation

With the objective of describing the seasonal spatial patterns in aerial effort, anchovy sightings and anchovy captures, the AMRMS files and the Southern California anchovy catch information were pooled by periods and seasons, and several distribution maps were prepared.

Reliable records of California commercial landings of the northern anchovy for all uses, including human consumption, dead bait, feeding in fish hatcheries and mink farms and reduction to oil and meal date from 1916. Landings for reduction purposes however, remained low during the first 30 years on record, never surpassing 3,000 tons. From 1947 until 1964 there were generally less than 10,000 tons harvested per year with the exception of the period 1952-1957 for which an average of 24,660 tons per year were landed when the Pacific sardine (*Sardinops sagax*) became very scarce in Southern California waters (see Table 5). In November 1965, the California Fish and Game Commission (CF&GC), authorized a 68,040 metric ton (75,000 short tons) anchovy harvest for reduction, and quotas ranging up to 150,937 metric tons (166,400 short tons) have been authorized since 1965. The year 1966, therefore, can be considered as the year the reduction fishery really began. Due to the lack of economic importance the first few years, capture remained low so the available information is not very good and it was decided to leave the years 1965 through 1968 out of most of this analysis.

Doyle Hanan (CF&G, comm. pers.), examined anchovy fishing logs and found very strong seasonal changes in catch per unit of effort, with catch per hour (a measure that appears to be more sensitive to availability), varying markedly from semester to semester. This result, in addition to the fact that until recently anchovy harvesting was traditionally a fall fishery (Figure 27), was the reason why it was decided to separate spring (April and May) and fall (September 15 to November 30) fishing seasons in this analysis.

Additionally, the years 1969 through 1982 were divided into three periods, keeping spring and fall fishing seasons separately. (Table 6). The first period comprises years 1969 through 1973, and it was characterized by a relatively low spawning biomass and a low fishing pressure, except for 1973 in which both the

Table 5. Yearly reduction California anchovy landings. From PFMC (1984). 1981-1985, Richard Methot (SWFC, Pers. Comm.)

Year	Landings (metric tons)	Year	Landings (metric tons)
1916	241	1951	3,154
1917	239	1952	25,303
1918	394	1953	38,935
1919	730	1954	19,237
1920	259	1955	20,272
1921	883	1956	25,819
1922	296	1957	18,392
1923	140	1958	5,263
1924	158	1959	3,254
1925	42	1960	2,294
1926	27	1961	3,498
1927	167	1962	1,254
1928	162	1963	2,073
1929	173	1964	2,257
1930	145	1965	2,600
1931	140	1966	28,250
1932	136	1967	31,575
1933	144	1968	14,096
1934	117	1969	61,362
1935	82	1970	87,310
1936	89	1971	40,690
1937	103	1972	62,687
1938	334	1973	120,327
1939	974	1974	75,040
1940	2,866	1975	143,800
1941	1,862	1976	113,327
1942	768	1977	101,131
1943	712	1978	11,457
1944	1,765	1979	53,244
1945	733	1980	49,037
1946	872	1981	52,011
1947	8,591	1982	43,742
1948	4,915	1983	2,854
1949	1,510	1984	1,722
1950	2,213	1985	0

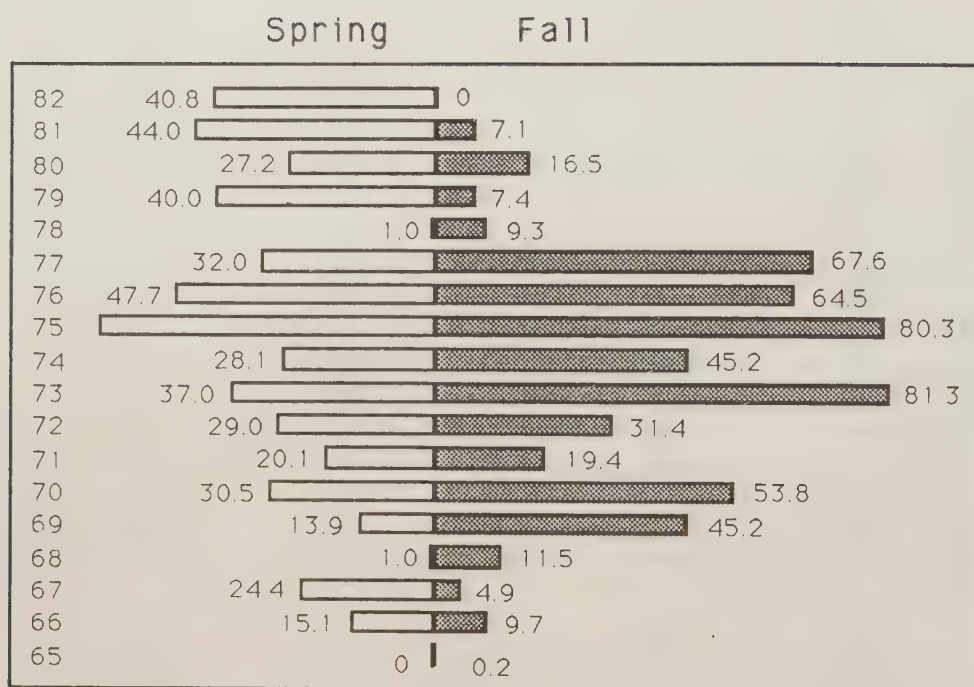


Figure 27. Seasonal anchovy landings, U.S. reduction fleet. Until 1978, Fall fishing was generally higher than Spring fishing.

Table 6. Average anchovy landings and spawning biomass. Summer harvest in México, shown here for comparison purposes, was high during 1978-1979, while the period 1974-1977 registered the highest spawning biomass and highest US landings.

	Average Biomass (1000 metric tons)	Average Landings (1000 metric tons)				Total
		United States		Mexico		
		Spring	Fall	Combined	Summer	
1969-1973	929.82	26.14	46.25	72.39	19.88	92.27
1974-1977	1902.55	42.29	64.44	106.73	78.26	184.99
1978-1979	669.66	20.53	8.34	28.87	206.44	235.31

biomass and the U.S. catch were large. The fall harvest in the U.S. was almost twice as much as that during the spring for the whole period. However, the participation of México in the fishery remained very low during these years. The second period, years 1974 through 1977 was characterized by a large spawning biomass averaging almost 2 million tons. This large biomass attracted the Mexican industry, which in this period began to exploit the anchovy in large quantities. Together, México and the United States accounted for more than 150,000 tons harvested on the average during these years. spring fishing was much larger in relation to fall fishing than during the previous period; but it was still some 30% lower. The third period includes the years 1978 through 1982 for the analysis done with the aerial survey files, and the years 1978 and 1979 for the maps done with fisheries data. These years were characterized by a low biomass averaging 670,000 tons, and also by a very poor U.S. harvest with an average of less than 40,000 tons. The spring fishery in this period was much higher than the fall fishery, perhaps due to the fishery on the Pacific mackerel which began to be substantially exploited in 1978, and is a much more profitable species than the anchovy. México, however, started to harvest anchovy during the Summer in large quantities averaging over 200,000 tons during the period, or more than 5 times the U.S. landings.

Table 7 shows the averages by year for sightings and effort during the aerial spotters activities for the seasons and years considered. This Table includes information for the whole area. The U.S. (seven selected boats) spring catch is about 50% lower than the fall catch, but seems to be fairly constant for the whole period. fall catch increased from 1969-1973 to 1974-1977; but without information on how many tons the selected vessels caught during 1978-1979 it is difficult to say there was a trend (catch for the whole fleet was 64,701 tons in these two years, which indicates very poor harvest, particularly in the fall). If the sampled vessels harvested their previous share (about 15%) of the total catch, their catch for these two years was not more than 10,000 tons, most of it caught in the spring fishery.

The number of sightings were not constant during the periods considered with the fall seasons being in general more variable and with more sightings than the spring season (70 more sightings in the fall on the average) during the whole period. The 1974-1977 period had a very high (420) number of sightings during the fall and a very low (150) during the spring and the 1978-1979 fall period a very low (147) number of sightings per year, perhaps associated with the relative abundance and

availability of anchovy schools, which was very low during 1978 and 1979.

The aerial effort (in number of block-flights) was approximately constant, and for the three periods considered, the fall season averaged twice as much effort as the spring season. The period 1974-1977 had a very low (1259) average of block-flights during the spring; but the average fall effort was comparable to that of other periods.

The variations in the number of sightings during the fall produced, however, some differences in the proportion of sightings per block searched. The proportion was relatively constant during the spring, with a slight increasing tendency; but varied strongly during the fall, with a low during the 1978-1979 period and a high during the 1974-1977 period. This pattern is perhaps reflecting the relative availability (visibility) of anchovy schools (spawning biomass) during those years, which was high in 1974-1977 and low during 1978-1979. In general, the highly increased effort during the fall season produced an additional very low proportion of sightings, when compared to the spring results.

Aerial Effort Distribution

The maps in Figures 28 and 29 show the spatial distribution of the aerial effort in a statistical grid of 10° by 10° squares used by the California Fish and Game Commission (CF&G). The general area surveyed during the spotters' activities extends from Point Sal to the Mexico - United States border and as far offshore as Tanner and Cortez banks. There are two main areas of aerial effort concentration. One is the Santa Barbara Channel zone, centered slightly west of Santa Barbara, and the other is the San Pedro Channel area, with center south of San Pedro Bay and usually extending to Santa Monica Bay. In general, the spring survey covers a smaller area when compared to the fall survey, and is less concentrated in the Santa Barbara Channel area. The San Pedro Channel region receives a lot of effort (particularly during the spring of 1974-1977); but a pattern started in the spring of 1978-1979 during which almost no attention was devoted to the southern area and most of the effort was expended covering the Santa Barbara Channel zone, especially during the fall, leaving the southern area to be surveyed mainly during the spring.

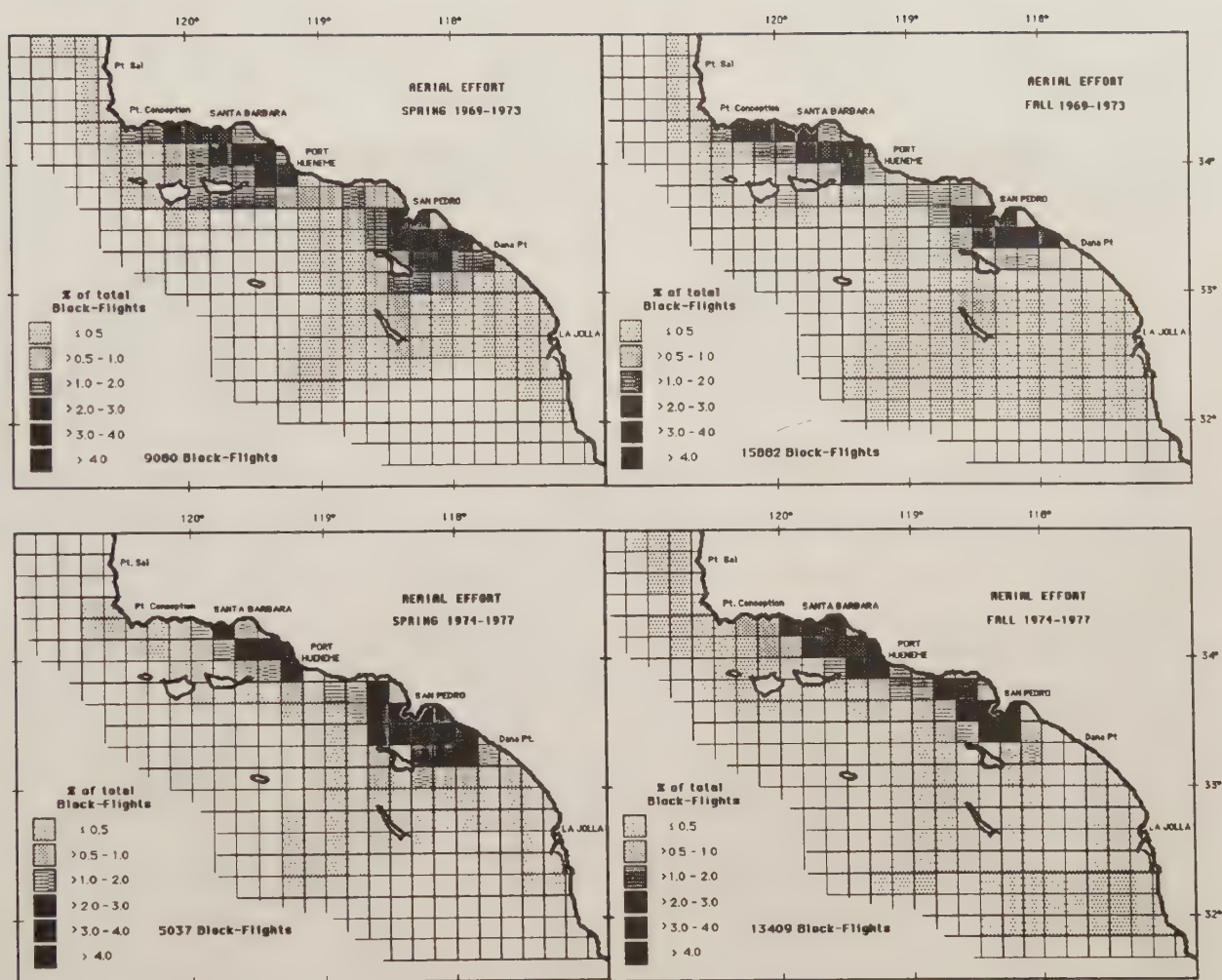


Figure 28. Aerial effort by seasons, 1969-1973 and 1974-1977. The maps show the spatial distribution of aerial effort on pelagic species in the Southern California Bight.

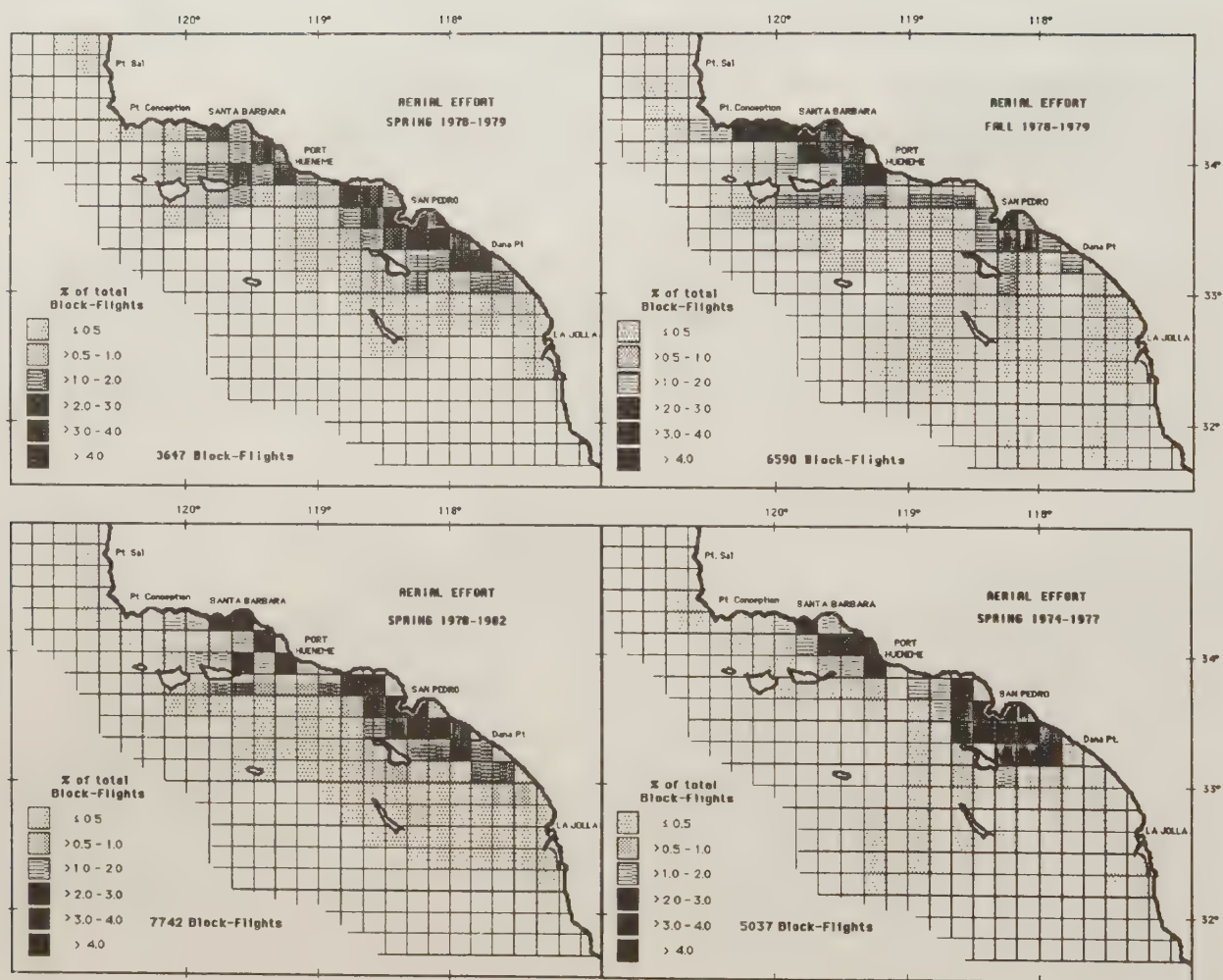


Figure 29. Aerial effort by seasons, 1978-1979 and 1978-1982. The maps show the spatial distribution of aerial effort on pelagic species in the Southern California Bight.

Anchovy Sightings Distribution

Figures 30 and 31 show the maps with the distribution of anchovy sightings made during the aerial surveys described above. In general, there are also two areas where the sightings are concentrated; but the Santa Barbara Channel region is not as well defined as it was on the effort maps (except during the fall of 1974-1977), so most of the observations were centered around the San Pedro Channel region. The spring and fall sighting areas are very similar and the general area where sightings were reported extends from Point Sal in the north to the border of the United States and Mexico to the south; but the area west of Gaviota is not very important, nor is the area south of Dana Point, except for a slight increment in inshore sighting activity during the spring of all periods. The general pattern is to sight the schools very close to shore (no further offshore than Santa Catalina Island), except for a few incidental sightings made around Tanner and Cortez banks during the 1969-1973 period. The schools were sighted in a clumped pattern around San Pedro Channel during the fall 1969-1973 and during both seasons in 1974-1977, with only a few sightings reported for Santa Monica Bay. The spring 1969-1973 sightings were more evenly distributed, weakly concentrated around San Pedro channel and the spring 1978-1979 observations were also uniformly distributed but with a stronger alongshore pattern, as sightings were reported from Santa Barbara to La Jolla. The fall sightings during this period were also evenly distributed but centered around the northern region and this pattern continued through 1982.

Distribution of sightings per aerial effort

Figure 32 shows the sighting per block-flight distribution maps for spring and fall during the period studied. The maps for the 1969-1973 seasons are very similar as they match closely the sighting maps for the same period (Figure 30). The aerial effort devoted to the Santa Barbara Channel area during the spring of 1969-1973 produced very few sightings, except very close to Santa Barbara, and a highly concentrated aerial effort in the San Pedro Channel region produced very even sightings per block-flight distribution, with slightly higher values in Santa Monica

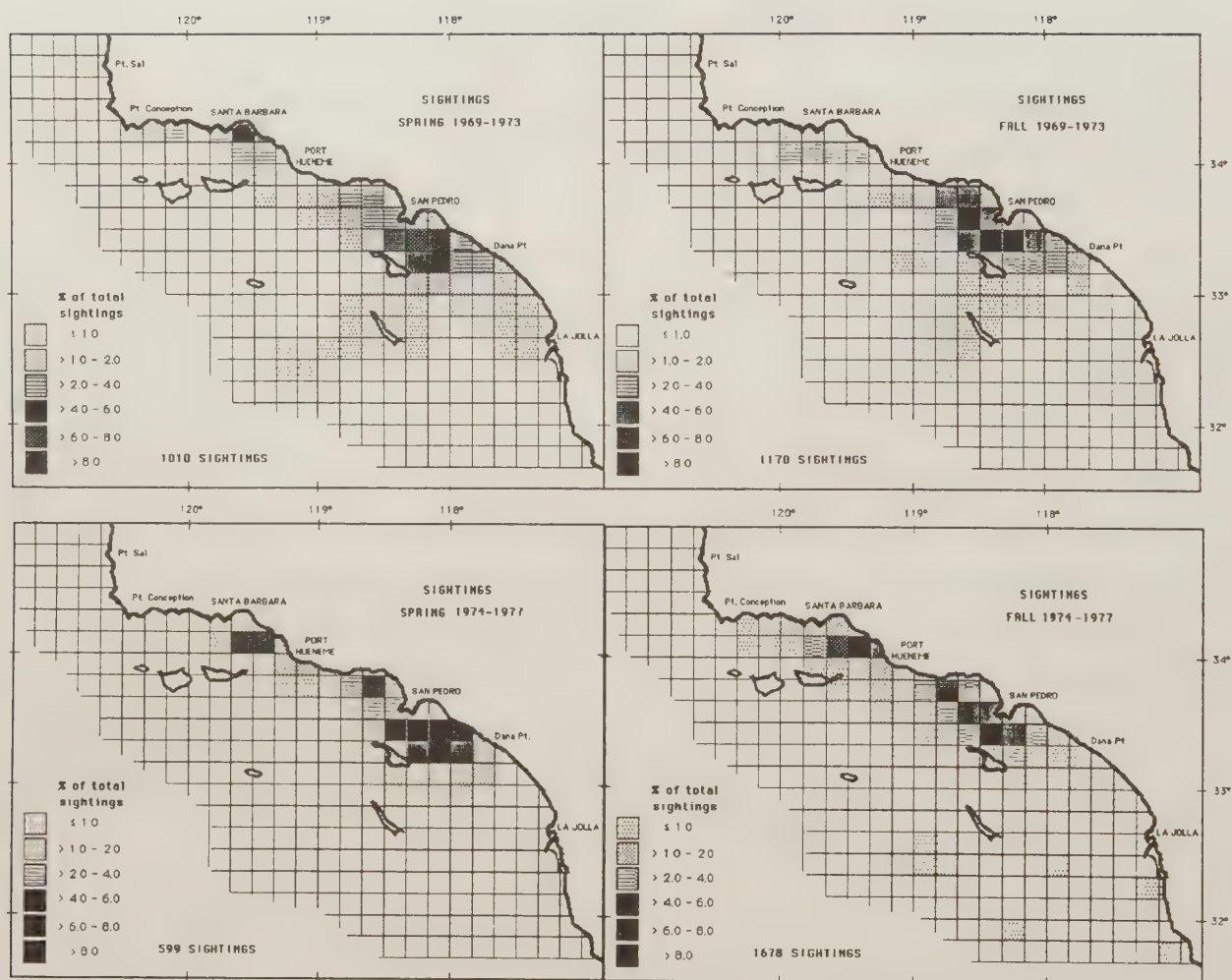


Figure 30. Anchovy sightings by season 1969-1973 and 1974-1977. The maps show the spatial distribution of seasonal anchovy sightings in the Southern California Bight.

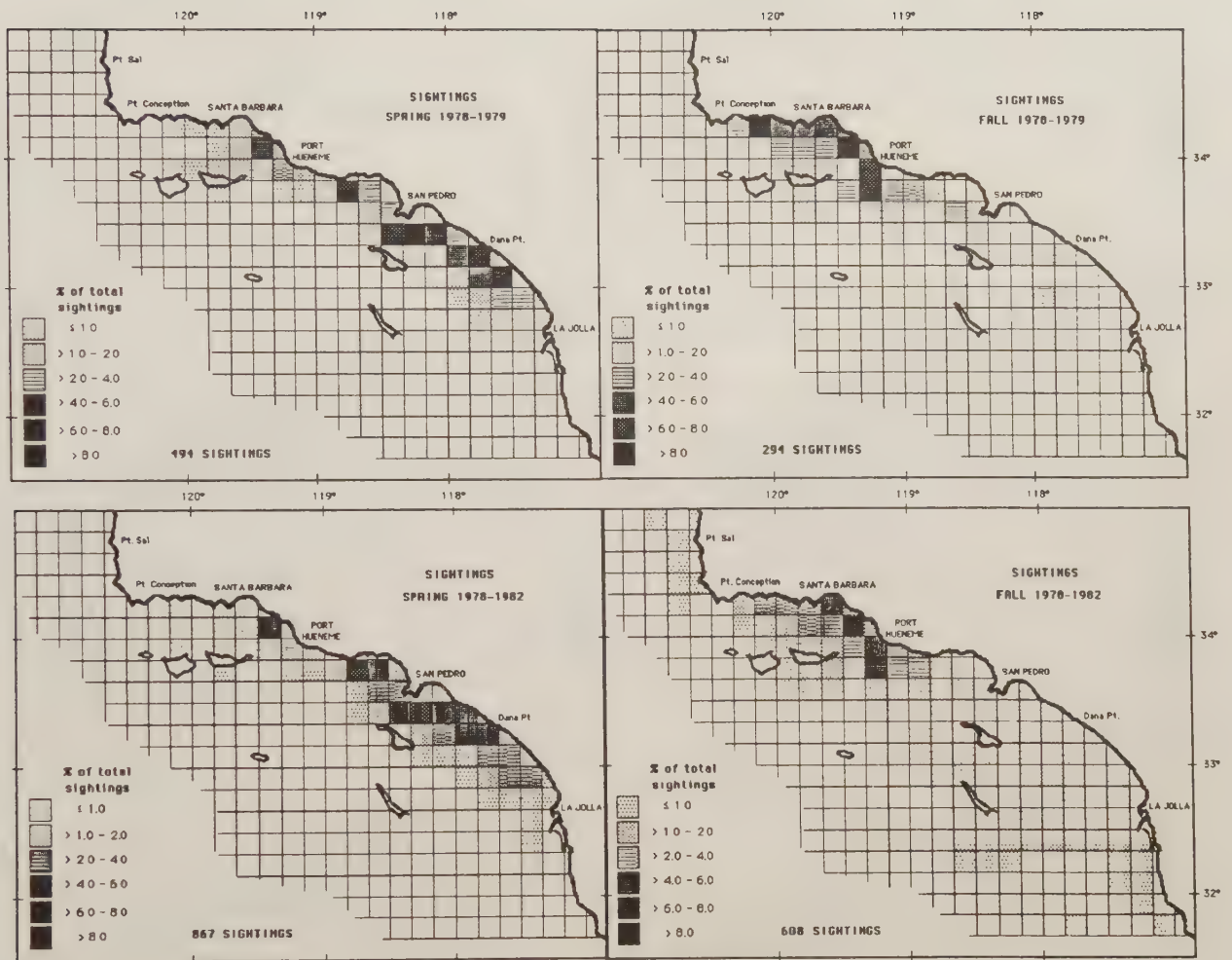


Figure 31. Anchovy sightings by season 1978-1979 and 1978-1982. The maps show the spatial distribution of seasonal anchovy sightings in the Southern California Bight.

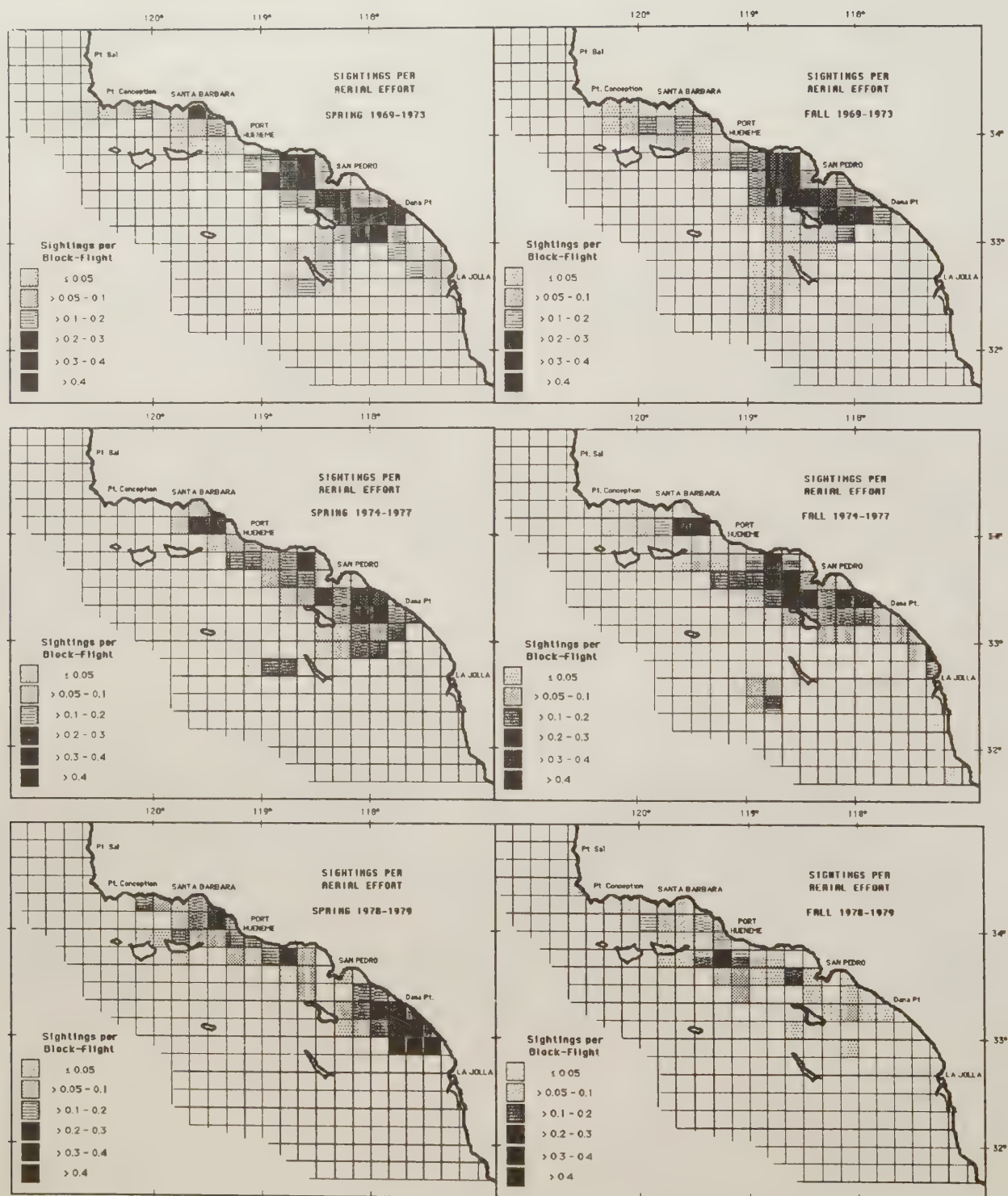


Figure 32. Anchovy sightings per aerial effort. The maps show the distribution of seasonal anchovy sightings per Block-Flight in the Southern California Bight for all the periods.

Bay. The fall 69-73 distribution is, by contrast, very concentrated in the northern end of San Pedro Channel and Santa Monica Bay. The great amount of aerial effort devoted to the northern area in this season produced almost no anchovy sightings, perhaps due to the fact that much of the fall aerial effort was directed toward Pacific bonito during this period. This species, more valuable than anchovy, declined later.

Sightings per aerial effort are more evenly distributed during the 1974-1977 seasons. The large effort concentration in the San Pedro Channel during the spring produced an even distribution, with somewhat higher number of sightings south of San Pedro Bay. During the fall of 1974-1977, large concentrations of schools were sighted south of Santa Barbara, but a large amount of aerial effort in the San Pedro Channel and Santa Monica Bay showed that sighted schools were evenly distributed. fall season sightings were reported closer to the coast than during the spring, but extending south to San Diego and the Mexican border. This pattern is just the opposite from that observed during the 1969-1973 period, when spring sightings extended south and somewhat closer to shore than during the fall season.

The 1978-1979 period shows a heavy concentration of school sightings per aerial block flighted south of Dana Point during the spring. However, aerial effort was concentrated again in the San Pedro Channel, as there were catches but no school sightings were reported in this area. The rest of the sighting per aerial effort distribution is uniform. The fall 1978-1979 distribution has shifted NW to the Santa Barbara Channel area, with large number of flights devoted to the coastal regions West of Santa Barbara. There were however no significant anchovy sightings reported, as the pilots were probably looking for other species during these years.

Distribution of Harvest

Maps in Figure 33 show the catch by block for the same seasons and periods described above. The maps were prepared using logbook information from the CDF&G and compiled by Doyle Hanan (pers. comm.) for seven representative vessels from the Southern California wetfish fleet. This information is comparable but it is independent from the aerial effort and sighting data of the surveys described before.

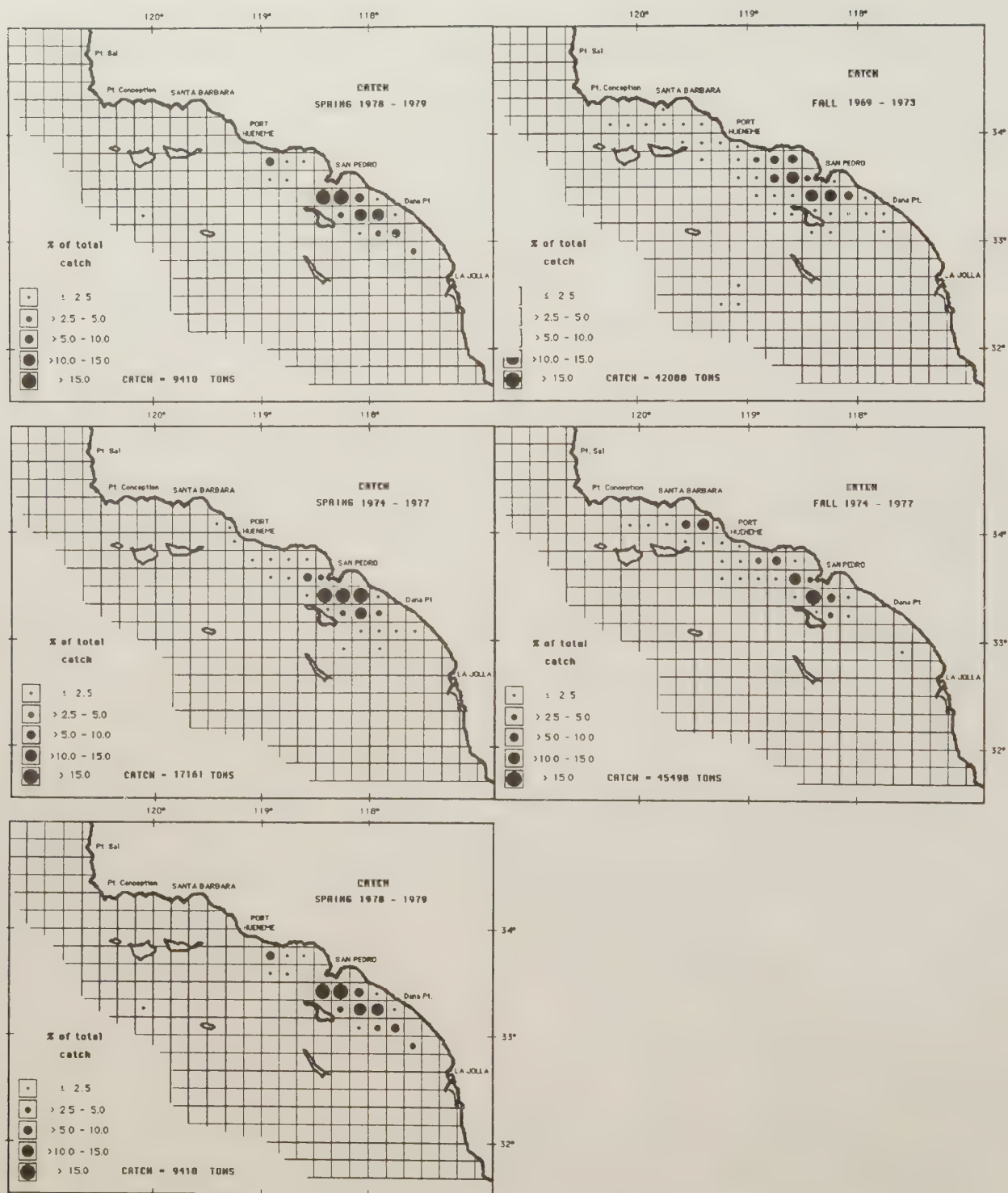


Figure 33. Anchovy landings by seasons. The maps show the spatial distribution of seasonal anchovy landings from the Southern California Bight for all the periods.

The generally exploited area extends from Point Dume in the north to Dana Point in the south; but the main harvest activity is centered around the eastern end of the San Pedro Channel area except for a slightly increased fishing activity during the fall season (particularly in the 1974-1977 period) along the Santa Barbara Channel. The spring fishing harvest is more concentrated in the San Pedro Channel area, and there is a tendency to extend the fishing grounds to the south of this region, particularly during the 1978-1979 period. This is opposite to the fall fishing pattern, since the harvest area in this season extends slightly to the north (Santa Barbara Channel region). It can be noticed that most of the catch comes from 4 or 5 statistical areas near San Pedro, which account for more than 60% of the total harvest during some periods. No catches were made offshore of Santa Catalina Island, except for a few schools caught at Tanner and Cortez Banks during the fall of 1969-1973.

The most important pattern observed from these distribution maps is the tendency to extend the fishing area to the south during the spring and to the north during the fall; but always maintaining the same harvest center in the area between San Pedro and Santa Catalina island. This tendency is also apparent in the sighting maps (Figures 30 and 31) and to a lesser extent in the aerial effort maps (Figures 28 and 29). The distribution of harvest is similar to that of sightings per block flight (Figure 32), except for some sightings near Santa Barbara, where no fishing was reported. This may be due more to differences in the boats sampled than to actual variation in school distributions (most of the time the boats sampled are based in San Pedro).

In summary, the 1969-1973 period was characterized by a great deal of aerial effort in the Santa Barbara Channel region that produced almost no sightings and a few school captures, particularly during the spring. This contrasts with the fall season, during which both harvest and sighting appear to be more related to the aerial effort. In general, as expected, harvest areas match closely sighting areas, except for a few sightings reported during the spring along the coast in the Santa Barbara Channel area that did not produce any reported harvest, and for a distribution of landings from the southern region which is not as concentrated as the sighting distribution, especially during the fall.

During the 1974-1977 period the general pattern seems to be very similar to that

of the previous period, with a large amount of effort in the Santa Barbara Channel area producing few sightings and less than 15% of the harvest. This pattern is particularly strong during the spring, as the fall aerial effort appears to be more related to both the sighting and harvest areas. The San Pedro Channel region aerial effort, however, matches very well during both seasons to harvest and sightings. The tendency to extend slightly to the south during the spring and slightly to the north during the fall can be appreciated both in the sighting and harvest area maps. Aerial effort, as well as the number of sightings and the harvest, is about three times higher during the fall season than it is during the spring period.

The 1978-1979 period was characterized by a good correlation between aerial effort and sighting areas, except that in the spring a few squares south of Newport Beach had some sightings from only a few flights in the area. During the fall, both sightings and effort are concentrated in the northern area, and the San Pedro Channel region has only a few scattered sightings reported. The harvest follows closely the sighting distribution during the spring (only season with active anchovy fishing by the selected boats during these years) and following the pattern of previous periods, extends south of the San Pedro Channel region, with only a few schools taken near Port Hueneme.

Considering the period from 1978 to 1982, the pattern of shifting the aerial effort to the Santa Barbara Channel region during the fall is even more evident and produced a high number of sightings in that area. The spring sighting distribution exhibits almost the opposite tendency, with no sightings reported in the northern area despite a high amount of aerial effort in the region. No harvest information is available from the boats selected for this period; but the annual landings for the whole fleet were very low in these years.

Concentration Rings in the Southern California Fishery

With the objective of studying some of the patterns associated with the use of space by the Southern California anchovy fishermen, the logbook information of the California Fish and Game Commission (CF&GC) was summarized according to the

distance from the fishing port (San Pedro) at which the harvest was made. The summaries were prepared for the years 1969 to 1973, and for spring (March and April) and fall (September 15 through November 30) seasons. Every CF&G statistical square has a characteristic distance from the fishing port (see section on distribution of areas as a function of distance from the fishing port), so the total catch, the number of sets, the area available to exploitation and the area actually harvested was associated to each distance and pooled within five mile intervals.

The results show that there is no capture reported for any square within three miles from the coast, as this area is closed to the reduction fishery. Therefore, capture within five miles from the coast is almost never reported, and it is considered to be incidental.

In the graphs in Figure 34 it can be seen that the capture during spring takes place as far as 55 nm from San Pedro; but in a very small quantity at distances greater than 40 nm. During the fall, no harvest was reported from blocks situated more than 40 nm from the fishing port. Both seasons exhibit the same general form and pattern, exploitation increasing up to a certain point, and then decreasing gradually. The spring harvesting peak (slightly less than 30% of the total catch) occurs between 15 and 20 miles from port, whereas the maximum for the fall season (also a little less than 30% of total harvest) is slightly closer to the port, at the interval 10-15 nm from San Pedro.

The graphs showing the number of sets (Figure 35) is very similar to the one displaying the proportion, but many more sets were made during the fall season. This season shows a peak of almost 300 sets made during the period 1969-1973 at the 10-15 nm interval, decreasing at a rate of about 50 sets every 5 miles. The spring peak is at the 15-20 nm range because the curve is shifted slightly to the right. The left side is also well developed with respect to the curve for the fall season, so that the 10-15 nm range is also very important, accounting for more than 150 sets.

The graph showing catch/area as a function of distance (Figure 36), presents a slightly different pattern. The highest ratio of catch/area fished is at the closer to home fishing port interval, and a continuous decline starts at this point, with an exception at 20-25 nm from San Pedro, where a slight increase is observed both during spring and fall, perhaps as a result of reduction in available area due to the Santa Catalina (which also has a protected area) and San Clemente islands. It seems that in general, fishermen tend to use more intensely the area closer to port.

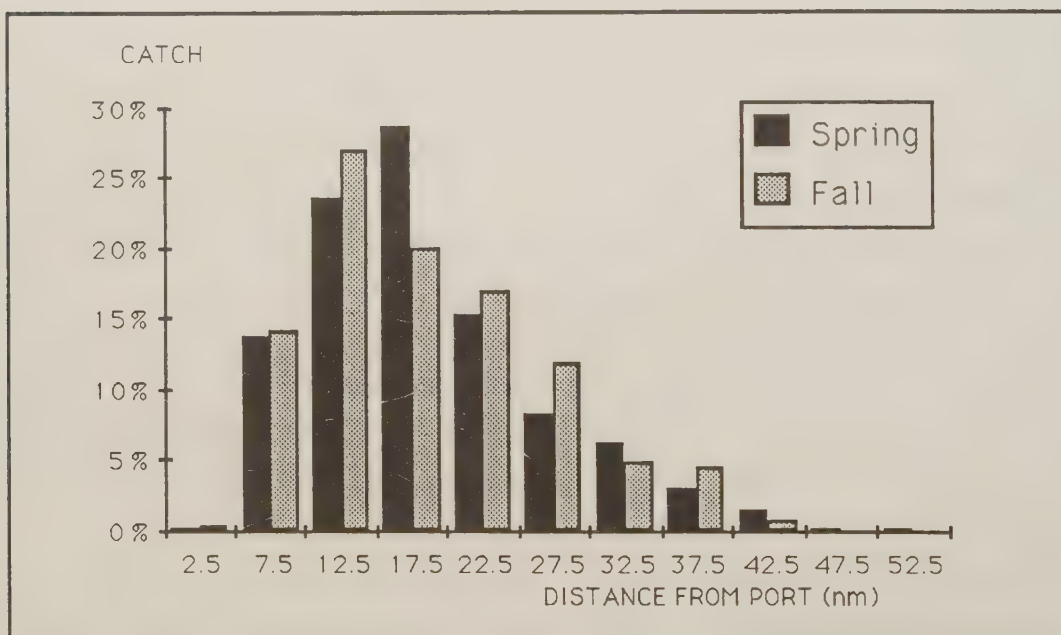
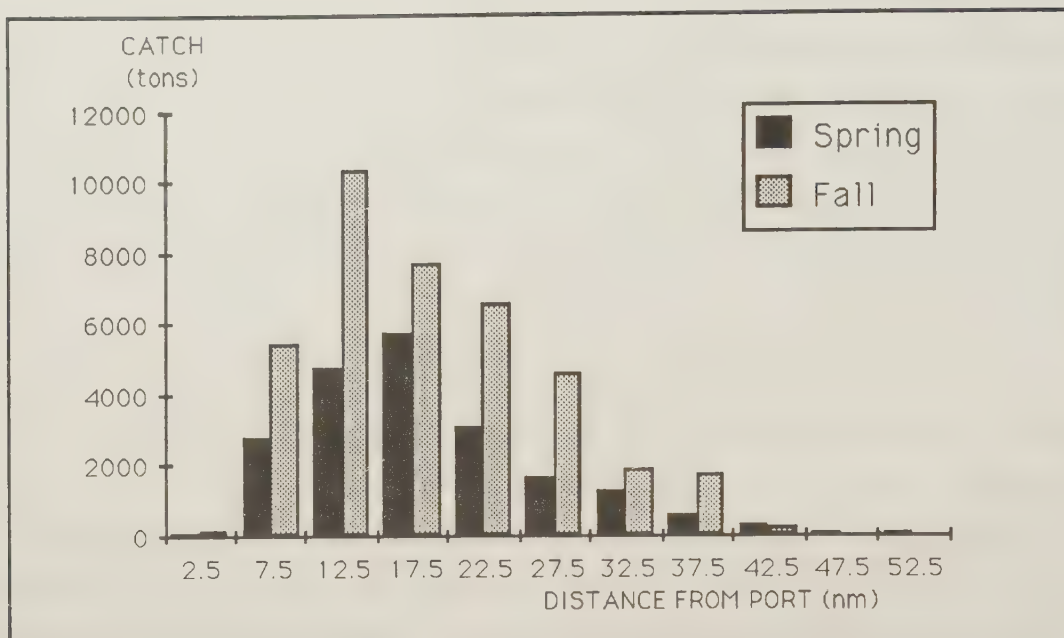


Figure 34. Concentration Rings; U.S. fishery landings. Concentration rings are very clear for landings. There is a peak between 12.5 and 17.5 nm from the fishing port, and a regular decrease at higher distances. Relatively more landings are made during the spring for the nearshore areas.

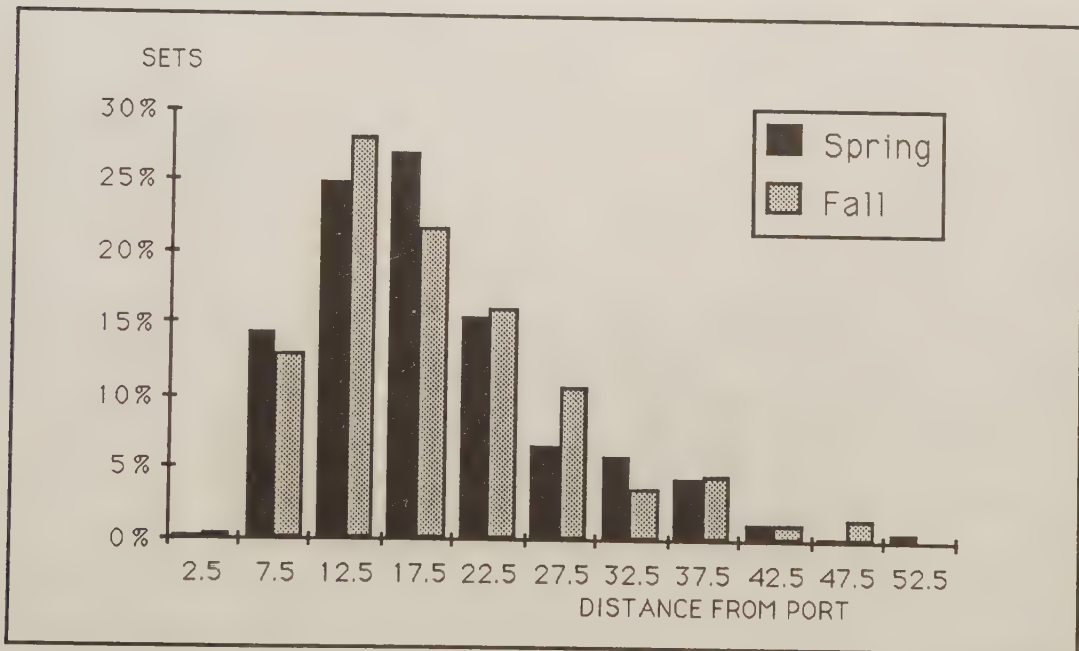
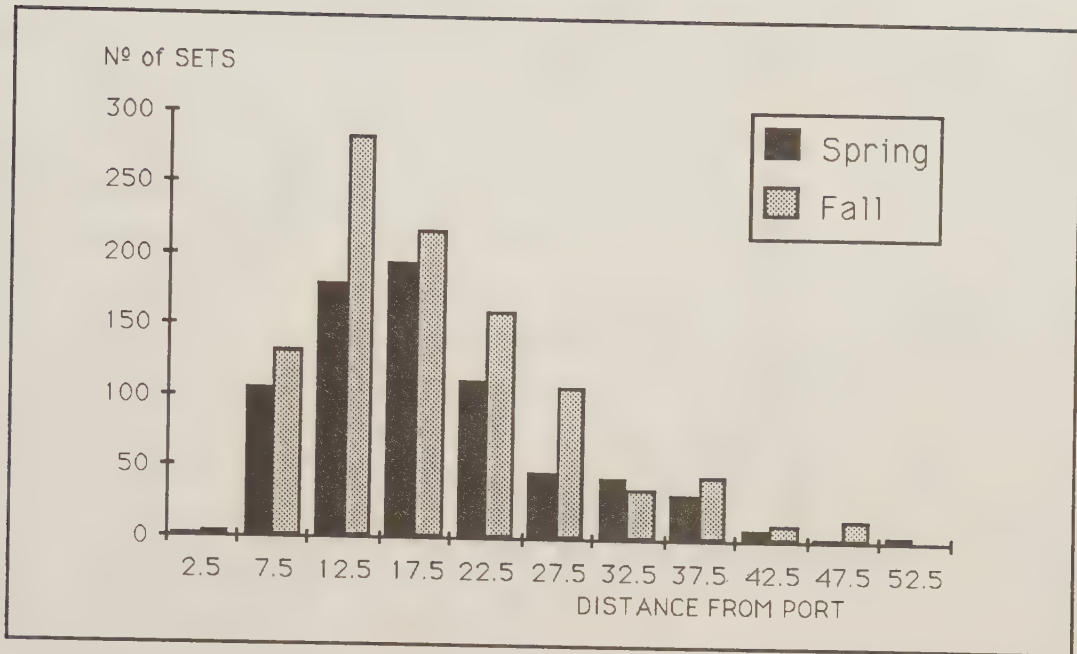


Figure 35. Concentration Rings; U.S. fishery number of sets. The upper graph shows the number of sets as a function of distance. Effort is more intense at the 12.5 nm interval during the fall. In the lower graph the proportion of total sets is shown; relatively more sets are made close to shore during spring.

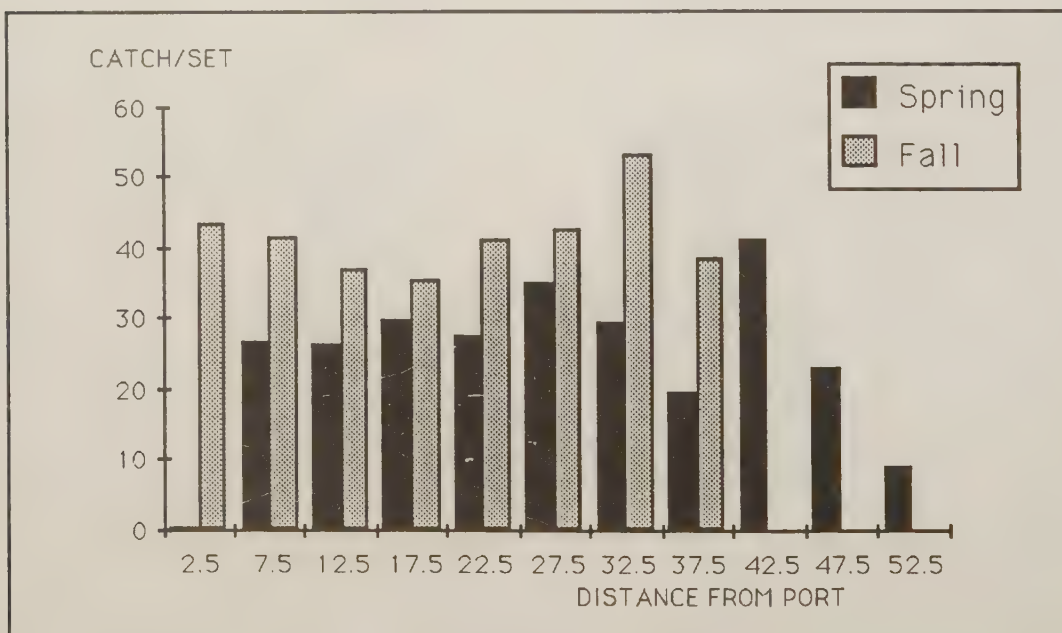
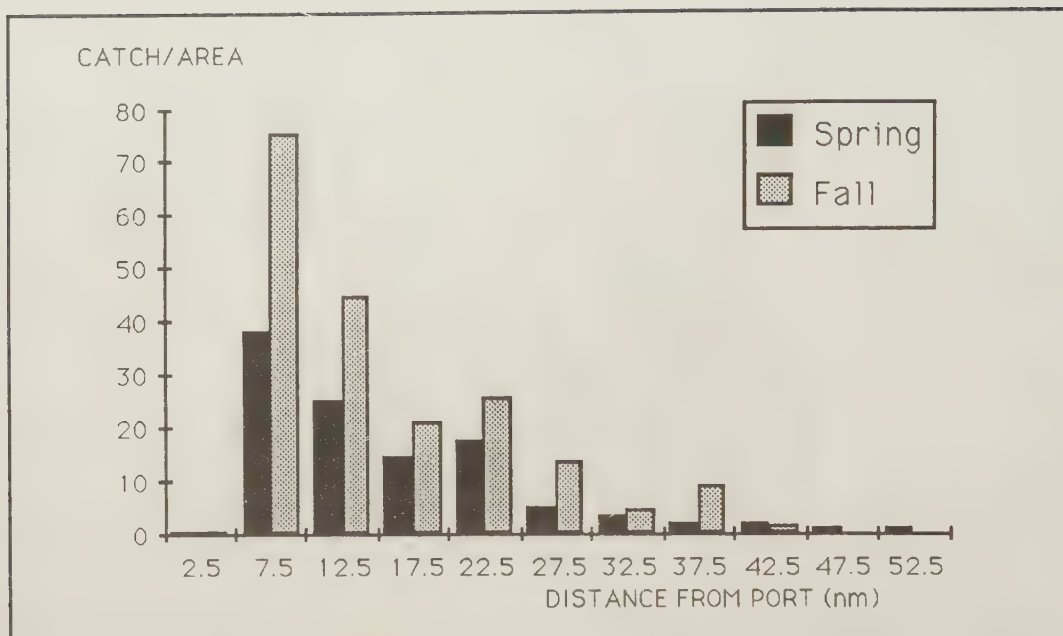


Figure 36. Concentration Rings; U.S. fishery catch per area and catch per set. Catch per set is higher during the fall, reflecting bigger schools during that season. However, this CPUE is not affected by distance. Catch per area falls off almost exponentially with distance.

Information on catch (tons) and effort (sets) combined as a catch rate is also shown in Figure 36. fall season has a higher rate of exploitation for all distance ranges, and tends to be approximately constant (41.4 tons on the average) despite marked differences both in catch and sets as a function of distance. The availability of bigger anchovy schools during the fall season can probably explain why catch per set is consistently higher at all distances. Spring season also shows a very steady pattern (average of 27.61 tons) up to 32.5 nm and then decreases, but since there were only a few sets made beyond this distance, it is hard to draw any conclusion. The main point is that catch/set has no relation with distance. This situation can be explained by the fact that cannery plants impose a catch limit to fishermen, which is usually less than vessel capacity. This limit varies according to fish meal price and plant capacity, but during these years remained approximately constant at 40 tons per vessel. It seems that fishermen fill up the vessels quota at all distance ranges, making catch/set not sensitive to changes in abundance as a function of distance from the fishing port.

A general pattern is apparent from catch and number of sets graphs and this is that fishermen are willing to harvest slightly farther away during spring than they do during the fall season (even though catch/set is lower), and as a consequence, spring catches maps show a somewhat more spread out spatial distribution. Peaks during fall for both catch and catch/area are also closer to the fishing port, and there is no reported catch at more than 30 miles from San Pedro during the fall.

The graph in Figure 37 combines the distribution of available area (up to 60 miles from San Pedro), with the catch obtained from those distance strata during spring and fall 1969 - 1973. Both spring and fall follow a similar pattern, except that during spring fishermen take some schools further offshore, but this distance stratum accounts for less than 5% of total catch (more than 40% of total area available). All the fall catch, and most of spring catch (96%) was harvested within 35 miles from port (55% of the area), with approximately 80% of the catch being harvested within only 20 miles from port (in only 20% of the total available area). Both spring and fall curves depart from the 45° line, indicating a high selectivity of the area fished, which produces a concentration of effort very close to the fishing port, particularly within the 20 miles inshore interval.

It is not clear whether the schools are more concentrated during the fall and less

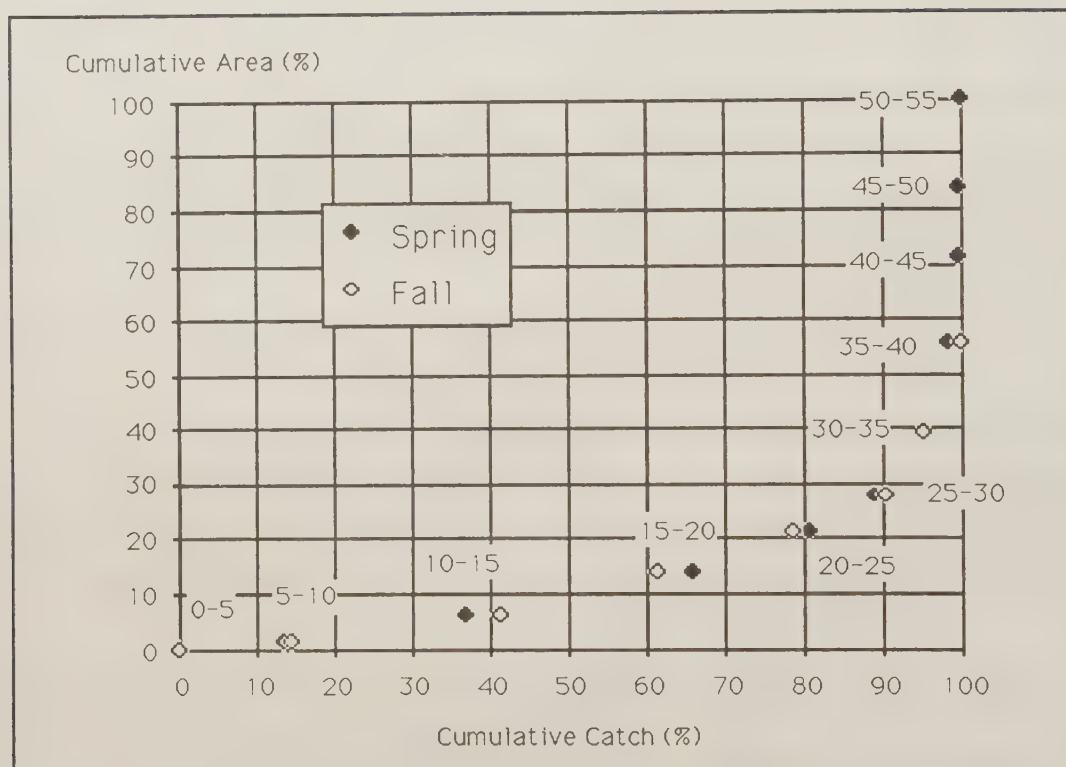


Figure 37. Relative landings and area exploited. Cumulative landings and the corresponding area exploited are shown as a function of distance from fishing port. Distance intervals are indicated next to each pair of points. Both spring and fall lines depart from the 45 line, indicating a high selectivity of the area fished.

clumped during the spring, causing the patterns shown for catch and distance, or if an alternative hypothesis could be more adequate to explain this behavior. However, data based on aerial surveys (both anchovy sightings and aerial effort) also show the same trends, indicating that anchovy behavior may be responsible for catch distribution, or at least be more important than non biological factors.

In addition, the general trend shown in the graphs suggests that if the area near the port were open (the area closed is 3 miles from shore, and at some places 5 miles), this area probably would be utilized heavily by the fishermen. Also, it is important to stress the point that there is no apparent relation between catch/set and distance, despite strong patterns in catch, sets and catch/area as a function of distance.

MEXICAN FISHERY PATTERNS

Although the Zapata company occasionally uses the services of spotter airplanes, there is no systematic data on aerial monitoring of pelagic schools in Mexican waters, so that it is not possible to compare aerial effort distributions with those of the U.S. fishery.

The Ensenada reduction anchovy fishing season begins generally in April and ends in January. However the bulk of the landings are made during the summer months, especially May, June and July. There is also a modest increase in activity around October. Since there were no clear seasonal or annual tendencies in either harvest or abundance, it was decided to separate the Zapata data only by individual years and months, not pooling over years or periods as it was done with the U.S. data.

Landings of the northern anchovy in Ensenada fluctuated between 4,000 and 40,000 tons between 1965 and 1974, averaging 19,600 tons per year. However, starting in 1975 both the fishing fleet and processing facilities in the port increased considerably; this factor, coupled with a period of high anchovy biomass (see Chapter I) produced a series of large captures, particularly during the late seventies and early eighties. Harvest in 1981 was almost 260,000 tons, and between 1977 and

1985 the average annual landings were up to 165,000 tons (Table 8).

Harvest Distribution

Maps in Figures 38 and 39 show the annual catch by statistical area landed and sampled at the Zapata company laboratories. The maps were prepared pooling information for the whole fleet over the entire year.

The exploited area extends from the U.S. border in the north to Punta Baja in the south. Fishing is usually restricted to the nearshore waters; very seldom the boats fish at more than 15 miles from shore. Production along the coast is not homogeneous; rather there are several localized areas which produce high catches every year. These spots are probably associated with upwelling regions: El Descanso and Salsipuedes north of Ensenada and the areas around Puerto Santo Tomás, Punta Colonet, Cabo San Quintín and Punta Baja in the south. Spatial distribution of harvest is however not uniform over the years, and it seems to be affected by oceanographic changes.

The distribution maps show that during 1978 the fleet harvested the coastal areas as far south as Punta Baja and never fished offshore, except near Ensenada. Most landings came from Salsipuedes and Santo Tomás areas. However, the sampling program began this year at the Zapata company, so there may be some irregularities in the sampling scheme this year.

There is no available data for 1979, but 1980 shows a similar distribution, although the landings sampled accounted for more than twice those taken during 1978. The distribution is more uniform and extends south to San Quintín, spreading somewhat offshore, especially near Punta Colonet but never more than 20 nm from shore. The most productive areas are again El Descanso and Santo Tomás, with some activity near San Quintín.

During 1981 most of the fishing activity was concentrated in Santo Tomás and the northern areas up to the U.S. border. Despite record landings in Ensenada (more than 250,000 tons, see Table 6), there were only a few landings from the southern regions of Punta Colonet and San Quintín. The Salsipuedes area contributed with more than 40% of total sampled landings. There are also some offshore landings from areas near Ensenada but the bulk of the fishing activity was centered in nearshore waters.

Table 8. Anchovy landings at Ensenada. The Zapata company harvests a large share of the total anchovy landed in Ensenada, probably more than 90%. Mexican landings started to increase during the mid seventies.

Year	Landings (metric tons)	Year	Landings (metric tons)
1965	9,171	1976	75,750
1966	13,243	1977	142,211
1967	20,104	1978	144,417
1968	14,267	1979	199,772
1969	3,871	1980	259,015
1970	27,977	*1981	258,700
1971	20,079	*1982	173,000
1972	32,640	*1983	87,000
1973	14,853	*1984	101,119
1974	39,826	*1985	118,770
1975	55,251		

* Zapata Landings only

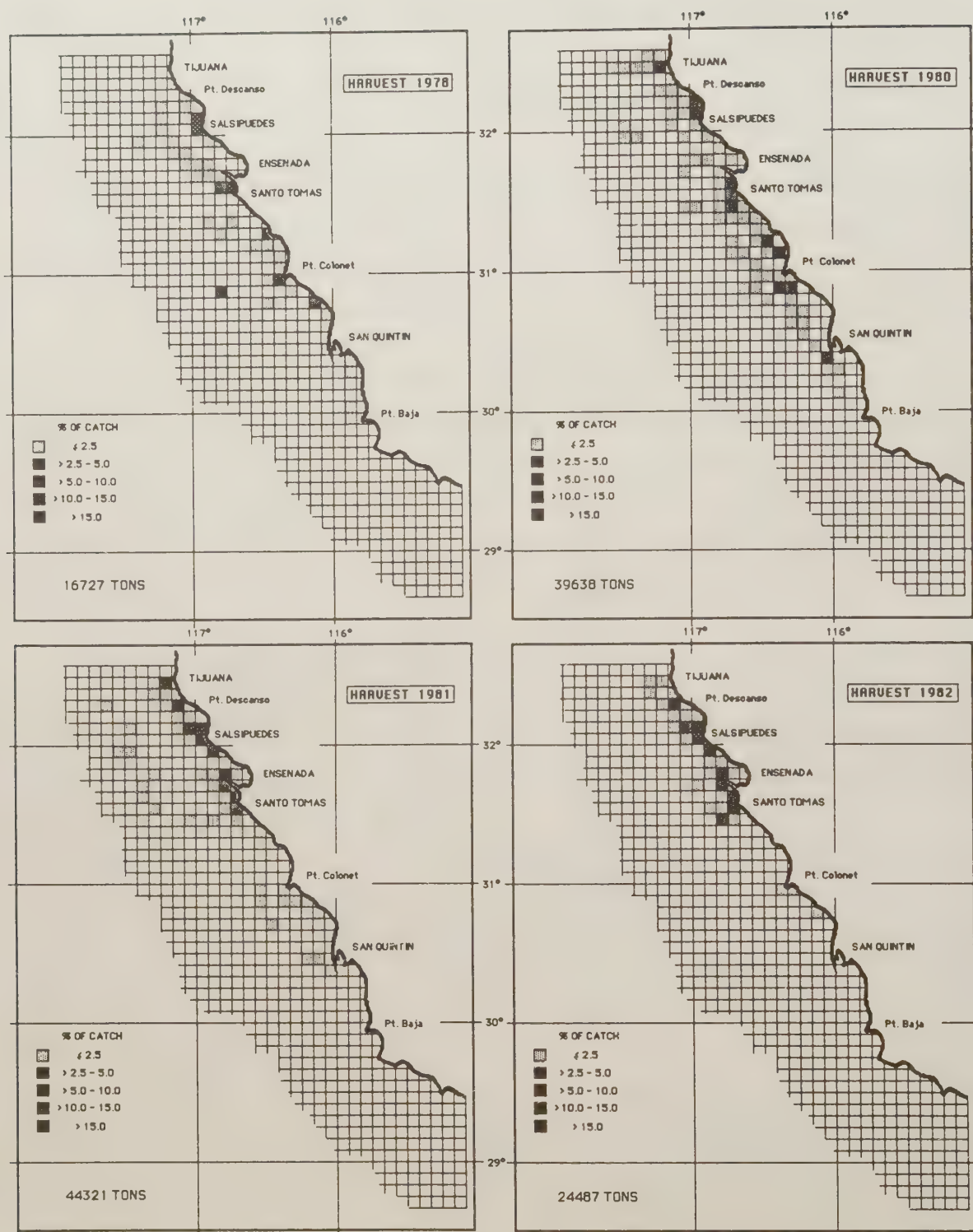


Figure 38. Ensenada anchovy landings by years 1978 - 1982. Highest landing seasons 1980 and 1981 were spatially different; harvest in 1980 was scattered, while harvest in 1981 came from the northern areas.

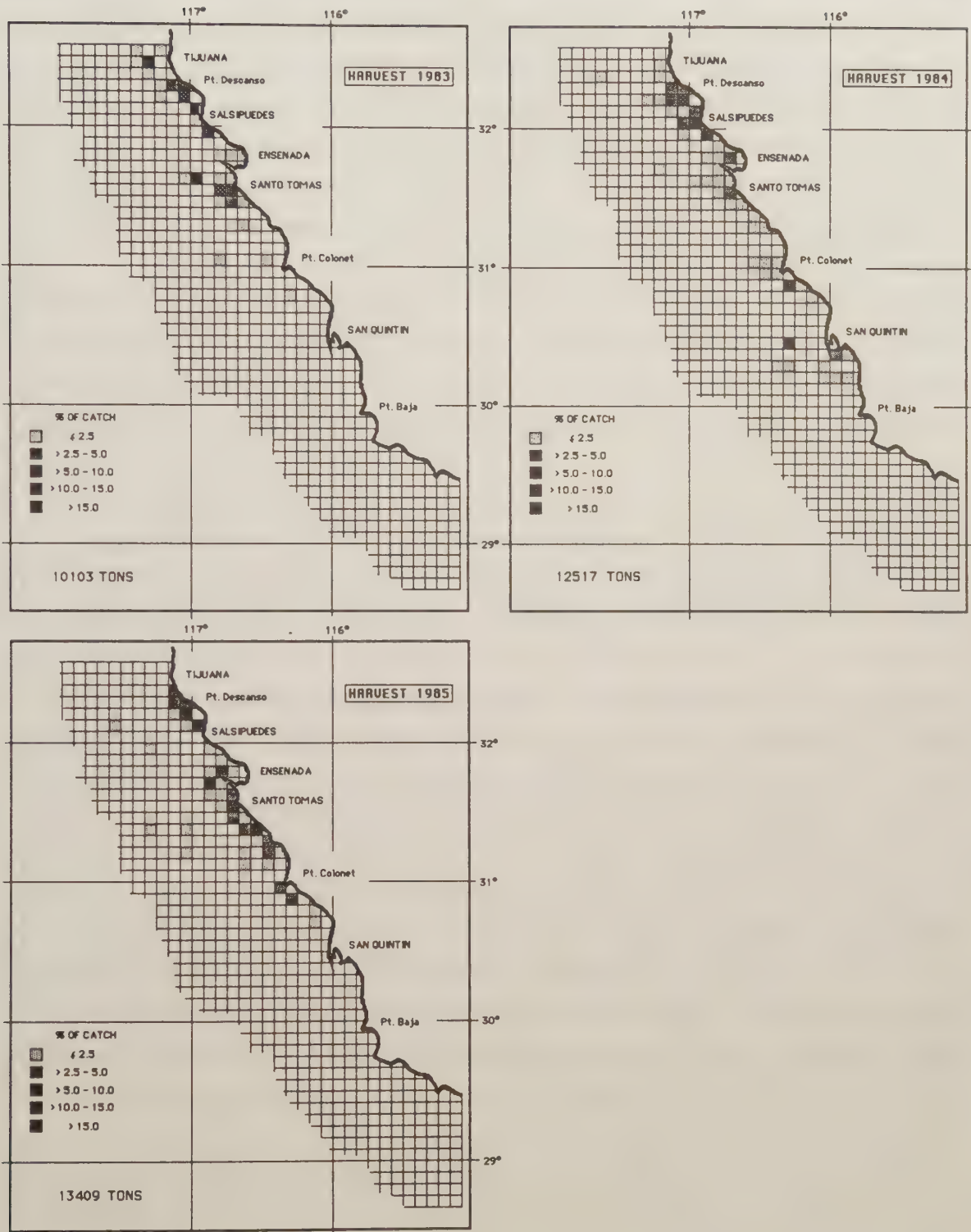


Figure 39. Ensenada anchovy landings by years 1983 - 1985. Harvest during El Niño 1982 (see Figure 38) and 1983 was restricted to the areas near and North of Ensenada. Catch during 1984 and 1985 was more dispersed.

By 1982 there was virtually no fishing south of Santo Tomás and no offshore harvest was reported this season. The area of Salsipuedes accounts for more than 25% of total landings. This year a very strong El Niño was suspected to have pushed north the range of many marine species due to abnormally high temperatures (see Wooster and Fluharty, 1985 and references therein for a summary of El Niño effects in the northern Pacific). This phenomenon probably affected harvest distribution as well as total landings which fell to 170,000 tons.

The following year, 1983, was similar to 1982; again catch was very poor in comparison to the previous seasons. Harvest distribution is very scattered and concentrated again in only two areas: El Descanso (45 % of total landings) and Santo Tomás (20 % of landings). Total landings decreased to 87,000 tons during this year. Again, very little activity was reported at the southern areas except for the Santo Tomás region.

By contrast, 1984 is much more similar to the pre El Niño years although landings remained somewhat low. The San Quintín and Punta Colonet areas contributed significantly again, but still the northern areas accounted for more of the landings sampled.

During 1985 the distribution is somewhat contracted with a relatively minor contribution from the northern areas and no fishing near San Quintín. The center of harvesting is now in the Santo Tomás area, just south of Ensenada, and this region accounts for a large proportion of catches.

In summary, the years previous to El Niño show a distribution extended to the south along the coast. However during El Niño of 1982 and 1983, the fleet used almost exclusively the northern areas and Santo Tomás. In 1984 and 1985 the patterns are similar to pre El Niño periods, especially 1984, but during 1985 the center has shifted slightly south to the Santo Tomás area. In general, offshore sets are rare and scattered and as expected, the most productive areas seem to be related to well known upwelling centers.

It is also important to notice that most of the northern landings are harvested at the beginning of the season, because the fleet gradually moves from the northern region to the areas near and just south of Ensenada as the season progresses. However, the new season begins mostly in the north (thus coinciding with the spring U.S. distributions), following a rotational pattern. This phenomenon will be discussed in more detail in the next chapter, when reviewing the optimal choice of

fishing areas.

Concentration Rings in the Ensenada Fishery

With the objective of describing some of the distance decay space use patterns by the Ensenada anchovy fishermen, the Zapata information was summarized according to the distance from Ensenada at which the capture was made. In this way, total catch, number of trips, catch per trip and catch per area fished (e.g. catch per statistical area fished) were related to each distance and pooled within five mile intervals for the years 1978 to 1985. The results are shown in Figures 40 and 41.

The landings versus distance graphs show that there is almost no capture reported within five miles from Ensenada, as the Bahía de Todos Santos is closed to the reduction fishery; harvest within the Bay is almost never reported and it is considered to be incidental. The vast majority of the catch is made between 15 and 40 miles from port, coinciding with the most productive areas of El Descanso and Santo Tomás. In general the distance decay distributions agree with the distribution maps (Figures 38 and 39) : distribution in the year 1978 is very irregular, with gaps at several distance strata. The years 1980 and 1981 are very spread out, but the peak of harvest is between 15 and 25 miles, while 1982 and 1983 distributions are spatially constrained; there is almost no exploitation of areas at more than 40 miles from Ensenada. The harvest concentration rings during the years 1984 and 1985 are very similar to the pre El Niño patterns, and the harvest peak has shifted to the region between 35 and 40 miles just south of Santo Tomás.

The number of trips made to each distance interval follows closely the harvest distributions, as there is a high correlation between landings and fishing effort (number of trips). The only exception is 1984, when a few trips to the 65-70 mile stratum produced a disproportionate amount of landings.

Due to the high correlation between harvest and effort, catch per trip seems to be constant over a wide range of distances, although it tends to be slightly lower near the port and higher at distant places. In general however, catch per trip is not affected by distance the way landings and trips are. This may indicate a largely constant local abundance of schools but as stated before, CPUE indices are not a good indication of abundance in pelagic schooling species. The effect may also be due to the tendency

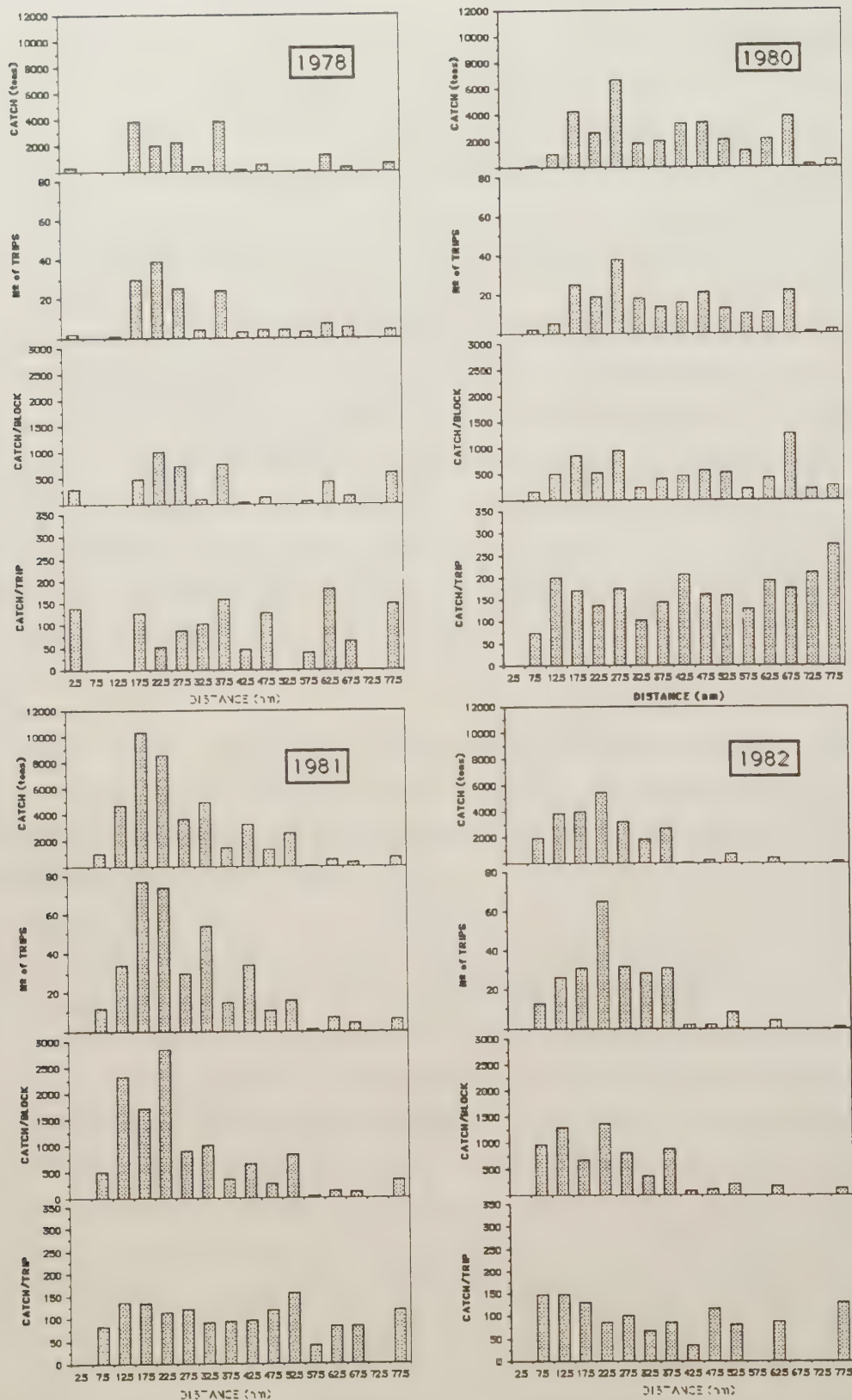


Figure 40. Concentration rings, Mexican fishery patterns 1978-1982. The year 1981 shows clear peaks at about 17.5 nm. Catch/trip appears to be constant within years.

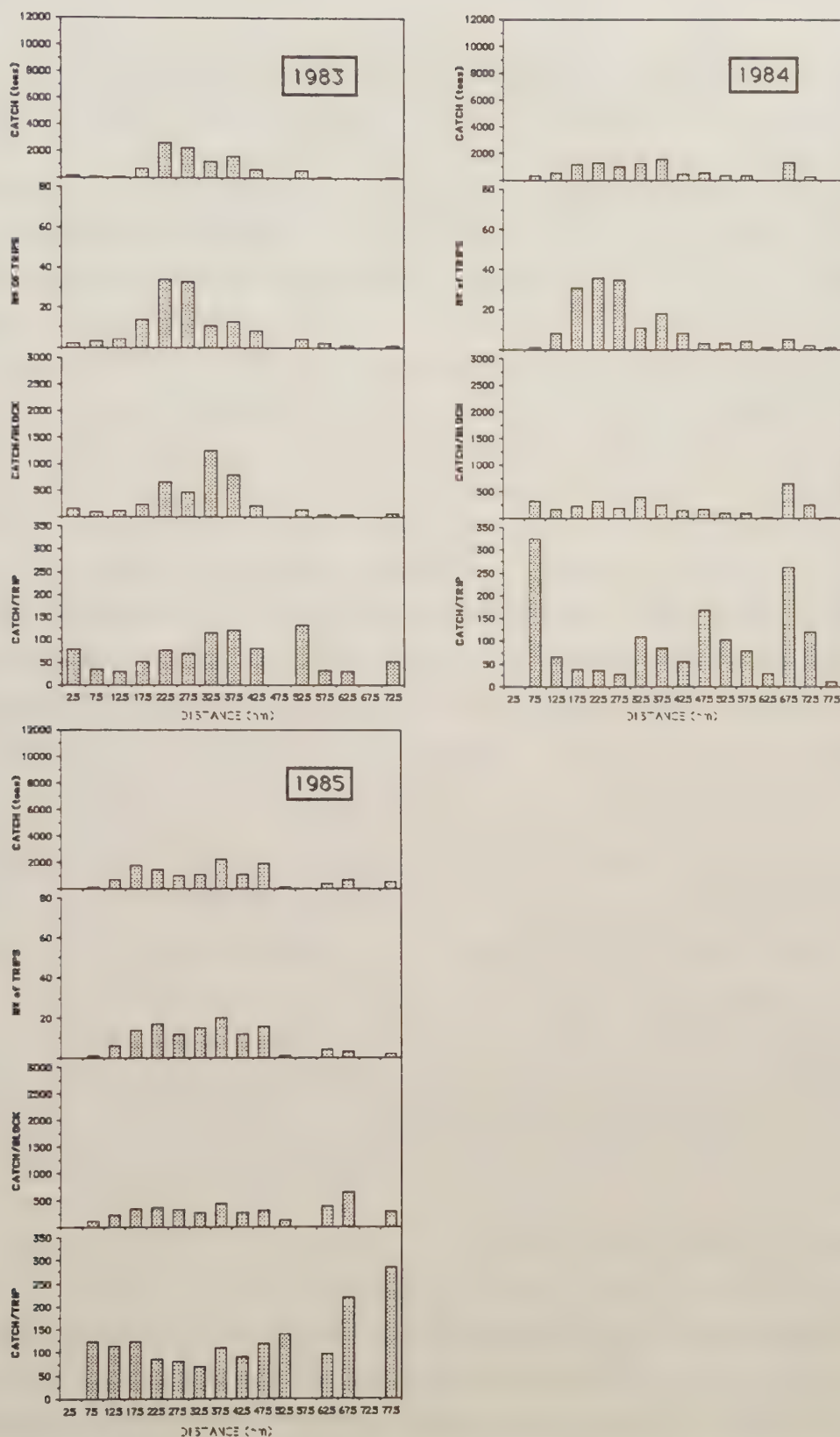


Figure 41. Concentration rings, Mexican fishery patterns 1983-1985. The year 1983 shows clear peaks at 22 nm; the pattern is not so obvious the other years.

of fishermen to select only 'worthwhile' schools regardless of distance from Ensenada. This possibility will be explored in detail in the next chapter on selection of optimal schools.

Catch per area fished is also seemingly uniform for most distances, although there is a peak between 20 and 30 miles from Ensenada during El Niño years and another at the 60-65 mile interval during non El Niño periods, where a few statistical areas show high productivity. The 20-30 mile peak in catch per area may be the effect of the México-US border in the northern fishing areas. However, productivity by area is not constant particularly for those coastal regions within 20 miles from port; there is a two to three fold annual variation in landings per block from the same areas.

In summary, the Mexican anchovy fleet shows a strong distance decay pattern in harvest, with a peak in landings from areas between 15 and 30 miles from Ensenada, although most landings come from places at less than 25 miles from port. The number of trips follows closely harvest patterns and as a result (although there is a slight tendency of the ratio to increase with increasing distance), catch per trip is largely independent of distance from Ensenada. Catch per block tends to peak at 25 miles, but there are also a few very productive areas at the 60-65 mile interval. However, annual productivity per area is highly variable, especially close to Ensenada.

III PATTERNS OF HETEROGENEITY : DISTANCE TRAVELED TO HARVEST

MEAN DISTANCE OF FISHING

Fishermen vary the place where they look for fish according to their experience and ability, but they also evaluate information on the abundance of the fish population itself, reacting to varying conditions (both biological and economic) by moving from one spot to another. Therefore, the use of information related to the distance (from the home fishing port) at which sets and sightings are made during

the fishing season can provide insight into those fishery aspects related to the spatio-temporal distribution of anchovy schools and fishing effort.

In the northern anchovy fishery, the large majority of sets are made very close to the fishing port, as was shown in the previous section on concentration rings. But to what extent are these spatial distribution patterns (e.g. the distance at which the sets are made) influenced by biological and economic factors ?

The mean (MDH) and standard deviation (SDDH) of the distance the U.S. and Mexican fishing boats travel during the fishing season to make a set was calculated to study this problem. The mean (MDS) and standard deviation (SDDS) of the distance at which the aerial spotters sighted anchovy schools during fall and spring fishing seasons for the U.S. fleet, was also computed. Distance to each statistical square was calculated as described in section II.

The time series of harvest by the U.S. seven selected boats includes years 1966 through 1979, except for the years 1967 and 1978 due to the small number of sets recorded during those fishing seasons. The aerial sightings and spawning biomass (SB) series comprise the years 1963 through 1982. Additionally, time series for the same years were also calculated for several fisheries and economic variables. These include : number of sets (NSET), number of sightings (NSIG), tons sighted per flight (TSIGFL), number of trips (NTRIP), catch per trip (CPTRIP), catch per set (CPSET), variance/mean of distance of harvest (VARMH), variance/mean of distance of sightings (VARMS), average fish meal price (AMEALP), average price of a ton of anchovy (ATONP), index of diesel price (DIESEL); and amount of fish meal imported to the U.S. (FMIMP). The same series were computed also for high and low anchovy biomass years, with the object of separating the effects of anchovy abundance. Low anchovy biomass years ($< 950,000$ tons) were 1968, 1969, 1970, 1971, 1972, and 1976. High anchovy biomass years ($\geq 950,000$ tons) included 1966, 1973, 1974, 1975, 1977 and 1979.

Following the same method for the Mexican data, a characteristic distance was assigned to each 5' by 5' statistical square used by the Ensenada-based Zapata Fishing Company (also described in section II). Mean distance of harvest (MDH), standard deviation of the distance of harvest (SDDH), number of sets (NSET), number of trips (NTRIP), number of statistical blocks exploited (BLOCK), catch per block (CPBLOCK) and number of trips per block (TRPBL) were also computed. The years included are 1978 to 1985, except 1979, year for which no data is available. Due

to the small number of years available and to the lack of large changes in spawning biomass, no separation of high and low biomass years was performed for the Mexican data.

Fishermen tend to concentrate very close to the fishing port, so that it is reasonable to think that they will travel large distances only when there are no “suitable” schools near the port (a suitable school is one with the correct size and behavior characteristics). Therefore, one of the simplest hypothesis to be studied is that the mean distance the boats travel decreases as anchovy biomass increases. This hypothesis implies that schools are most dispersed when biomass is low, forcing fishermen to travel more to find adequate fish concentrations, or equivalently, it assumes that searching time is an inverse function of school density (i.e., number of schools per square nm). The hypothesis can also be applied to the sighting distances, as the pilots usually scout anchovy schools for the commercial fleet. However, it is possible that both the mean distance and standard deviation of sightings may be higher than the mean distance and standard deviation of harvest, due to the pilots’ tendency to scout a little more offshore ‘just in case’, sometimes reporting schools that are far away from port and outside of the range of operation of the fleet. This tendency is expected, given the larger domain of action of the airplanes. These ideas form the basis of the second hypothesis, which is whether the mean distance the boats travel is equal to the mean distance schools are seen, independently of anchovy abundance. Under this equality hypothesis, one expects that the ratio of the two means would be close to one and constant over a wide range of biomass levels. These hypotheses were studied for both the Mexican and the U.S. fleet using the correlation coefficients among variables, simple regression between pairs of variables, and by looking at the variation over time. Also, in order to separate the effects of large biological and economic components, a factor analysis was performed using the Southern California data.

Southern California Fleet

Correlation coefficients

Table 9 shows the matrices of correlation coefficient among variables for all the

years and for years of high and low anchovy biomass separately. Coefficients in bold are significant at the 0.05 probability level and underlined coefficients are significant at the 0.1 level. The rest of the coefficients are not significant.

It is interesting to notice that spawning biomass (SB) and harvest are positively related for the three series and that both variables are correlated to NSET, NTRIP and NSIG. SB is also negatively related to MDS and SDDS while the relationship to harvest is somewhat weaker, but showing the same tendency. SB shows also some association with SDDH which is lacking for harvest. In general, both spawning biomass and harvest show approximately the same pattern for high and low periods, but SB tends to be more related to MDS and SDDS while harvest is more related to NSET and NTRIP for both high and low biomass series. SB and harvest are also positively associated to CPTRIP and to some extent to CPSET during low abundance periods. This implies that CPSET remains largely constant, particularly during low abundance years; this is probably due to the cannery limits discussed in the previous section. Obviously, during low abundance periods it takes more trips to achieve the same harvest amount.

From the coefficients alone it is not possible to determine whether the schools are closer to shore during high density years (although it is very likely), or if the pilots simply do not want to look further offshore for anchovies, since the schools can be spotted and be easily captured near the fishing port.

MDH is positively associated with SDDH and MDS during high abundance years but not when abundance decreases. On the other hand, distance of harvest shows some positive correlation with NSIG and CPTRIP only for low abundance periods. MDH does not show a strong relation with any of the remaining variables. Therefore, the degree of dispersion of captured schools increases with the distance traveled to harvest them, but only when biomass is high. When biomass is low, a better indication of the distance fishermen have traveled is the number of sightings and the capture by trip. In addition to being associated with MDH, SDDH is also positively related to MDS and to CPTRIP but only during high abundance periods.

On the other hand, MDS is always positively correlated to its standard deviation SDDS, so the schools are always more dispersed when sighted far away than when they are closer to shore. MDS is also negatively but not too strongly related to NSET and NSIG. As it was the case with MDH, the distance of sightings is also strongly correlated to CPTRIP during high biomass series. Again, CPTRIP is

a good indicator of the distance at which schools have been sighted, while its relative importance decreases when schools are sighted far away during low abundance years. The degree of dispersion of sightings is also somewhat related to NTRIP during high biomass and to NSET during low abundance periods.

As we have seen, the raw effort (NTRIP, NSET and NSIG) counts are usually correlated to the same variables and positively correlated among them, particularly NSET and NTRIP to NSIG during high abundance years. In addition, there is a strong positive relationship between the abundance indices CPSET and CPTRIP during low abundance periods but non significant and negative during high biomass periods.

In general, the low abundance years tend to have fewer significant coefficients than the high abundance periods. Both series, however tend to exhibit the same relationships among variables, except for the following cases (none of them is significant): CPTRIP shows a high, positive association to biomass and CPSET but only during low abundance periods, making this index a good indicator of abundance when schools are closer to shore and fishermen do not need to travel too much. Also, the degree of dispersion of sets made by the fishing fleet is associated very strongly with MDH, MDS and CPTRIP during high abundance periods, but shows no relation or a negative, non significant tendency when abundance is low. This is perhaps indicating a larger average size of schools when dispersion (and hence abundance) is higher, since CPTRIP increases with higher SDDH.

In summary, harvest and biomass are related to the same groups of variables. A "raw effort count" group formed by NSET, NTRIP and NSIG, and an "abundance index group" made of CPTRIP and CPSET can also be distinguished. The rest of the relationships among variables are not very clear from the correlation matrices alone.

Mean Distance and Biomass

Figure 42 shows scattergrams of mean distance of harvest and sightings (and the corresponding standard deviations) versus anchovy spawning biomass. In the plot

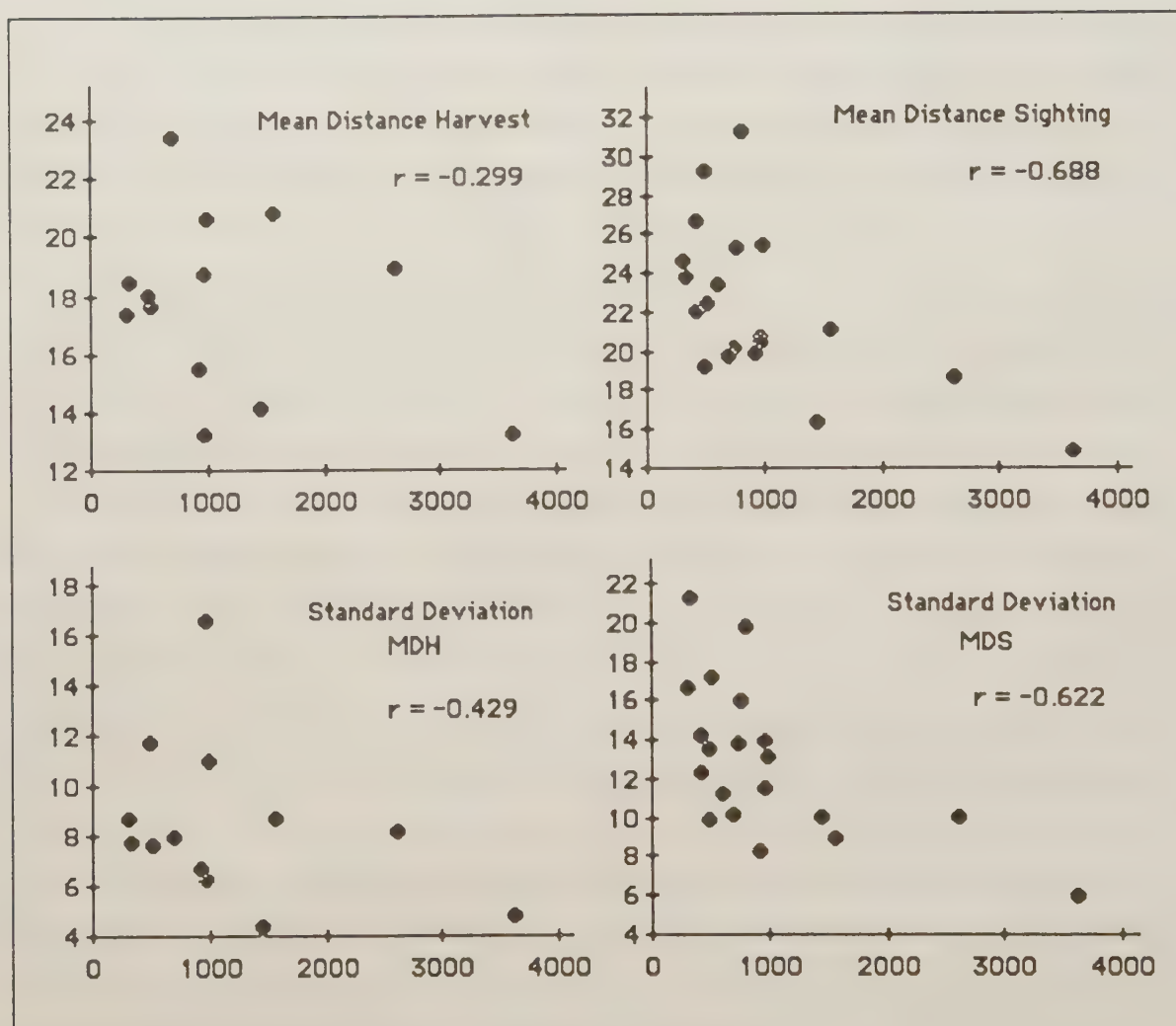


Figure 42. Mean distance of harvest and sightings and anchovy biomass. Anchovy spawning biomass (1000 tons) is shown in the x axis. Standard deviation of MDH and MDS and biomass is plotted in the lower two graphs. MDH has the lowest correlation coefficient.

of MDH and SB, the values are very dispersed and the correlation coefficient is low ($r = -0.299$, n.s.), but there seems to be a certain decreasing tendency of MDH at very high SB levels. When only high biomass years are considered, r is even lower ($r = -0.261$), but it increases to 0.409 for low biomass years, changing direction. The overall correlation indicates however, that there is no simple relation between MDH and SB. In fact, as it was shown above, MDH is not correlated to most of the variables considered. The high correlation of MDH to its standard deviation during high biomass years is probably indicating that the degree of dispersion of schools is higher at great distances. This agrees well with the idea of concentration rings or distance decay patterns, and indicates that the anchovy tends to form schools whose density is higher in the coastal zone during these periods, thereby attracting fishermen to concentrate in that area.

The plot of SDDH in Figure 42 shows a somewhat stronger relation ($r = -0.425$, $p = .084$) to spawning biomass. The coefficient is negative, indicating that fishermen tend to make sets closely spaced when abundance is high. Therefore, they do not just stay close to the fishing ports under these conditions, but they do so in high concentration, and tend to travel more and to be widely spaced at medium and low biomass levels, as expected. This agrees well with the idea that searching time is an inverse function of school density, which diminishes during low abundance years. The pattern is maintained during both high ($r = -0.402$) and low ($r = -0.210$) abundance periods, but the relation is not significant for these years.

The scatterplot in Figure 42 shows the relation between MDS and SB for 20 years of sighting data. The negative relation of sighting distance to biomass is clear ($r = -0.688$, $p = .007$), and it is apparent that the distance at which the schools are detected is on the average much smaller for years of high abundance (e.g. 1975); the smallest MDS was recorded during the year with the highest abundance. There is a large dispersion of MDS values (as it was the case with MDH values) at abundance levels below one million metric tons. High ($r = -0.723$, $p = 0.052$) and low ($r = -0.849$, $p = 0.016$) abundance series show the same pattern, MDS decreasing with increasing biomass. The standard deviation of sighting distance (SDDS) and biomass plot in Figure 42 is very similar to the MDS graph ($r = -0.622$, $p = 0.015$). The lower standard deviation was also recorded in 1975, the year of higher abundance. As it was the case with MDS when the biomass level drops below one million metric tons, the data become very scattered, with SDDS as high as 22 nm at abundances below 300,000 tons. Again, low ($r = -0.772$, $p = 0.036$) and high ($r = -0.859$, $p = 0.014$) abundance series show the same

strong pattern of decreasing standard deviation of sightings with increasing biomass.

It is interesting to point out that the relationship in both harvest and sightings cases looks like an exponentially decreasing function, showing large changes in MDS with slight increases in biomass (when SB is below 920,000) and small changes in MDS with large biomass changes above 920,000 tons. The general pattern of these relationships indicates that anchovy schools are seen, and to some extent harvested closer to the port and highly clumped during high abundance periods. The situation is less clear during low spawning biomass years but it can be said that the pilots tend to detect anchovy schools at higher distances and slightly more dispersed during these periods.

Mean Distance over Time

A look at the data over time shows some patterns that help to explain to some extent the correlations (Figure 43). Spawning biomass remained relatively low (less than 1 000,000 tons) until 1972. After this year there was a sudden increase, reaching a peak in 1975 and declining again later below one million tons, with less than 500,000 tons in recent years. MDS is well correlated to the number of sightings because there was a decrease in the distance at which the schools were spotted during the mid-seventies, when spawning biomass was high, and an increase during the early eighties when spawning biomass decreased below one million tons. As was shown above MDH is not highly correlated to SB, but there is a close correspondence some years. There is also a decrease in MDH during the mid seventies and then an increase until 1979, last year of fisheries data. This explains why MDH and MDS are well correlated.

The late sixties was a period of relative stability for both spawning (with a decreasing tendency) and MDS. The mean distance of harvest was also relatively constant, except for the low value of 1966 but since this was the first year a large commercial fishery operated, many non biological factors such as learning may have influenced the distance at which the boats harvested. It is also important to notice that MDS is consistently higher than MDH for all years except 1969 which is the highest value recorded for the mean distance of harvest.

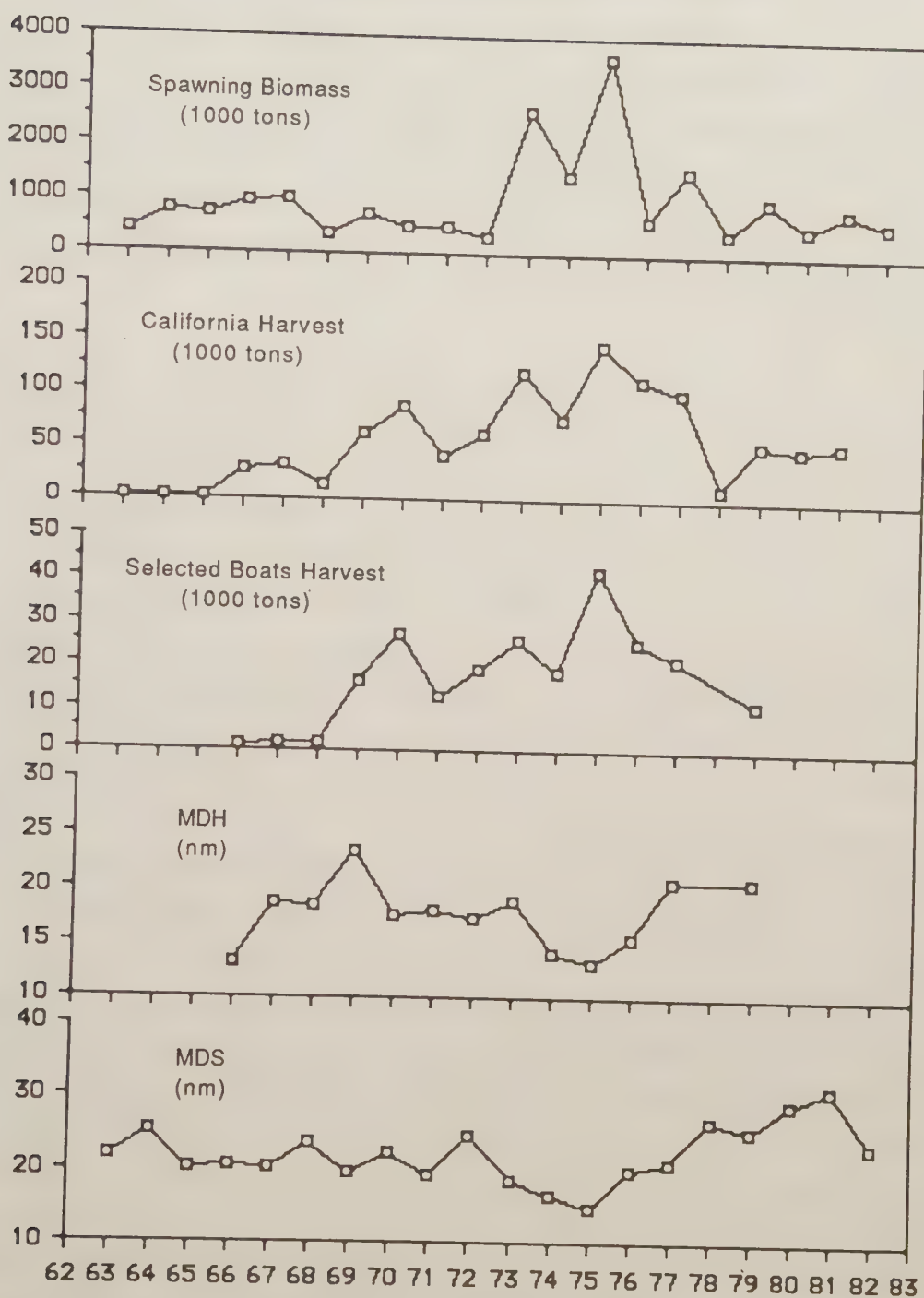


Figure 43. Biomass, landings, MDH and MDS, U.S. fishery 1963-1982. Spawning biomass and landings show an increase during the mid seventies. Highest point in landings by selected boats (1975) coincides with lowest mean distance of harvest and sightings.

Total harvest by the selected boats follows closely harvest for all California until 1976. After that year total harvest declined abruptly while the catch from the selected boats declined more slowly. Both series however, are closely related ($r = 0.95$) and correlated to spawning biomass ($r = 0.70$ to total harvest and $r = -0.63$ to catch from the boats studied). This relation is particularly good during the mid seventies, when spawning biomass was large. However, during 1969 and 1970 both series show an increase despite the fact that anchovy abundance remained approximately constant at 500,000 tons that period.

Monthly mean distance sightings time series (Figure 44) shows a high variation in MDS, with the higher peaks during the summer, which in Southern California is a non anchovy fishing season. Therefore, the peaks indicate that there were schools at those distances during the summer months, but since the pilots were not looking specifically for anchovy, these sightings may be regarded as incidental.

There is a tendency for both the variance and the peaks to be smaller during the mid seventies, coinciding with high anchovy spawning biomass. After 1977 there is a tendency of MDS to increase and the data become very sparse for the last years. The monthly mean of distance of harvest is even more sketchy (Figure 45). However a decline in MDH can also be observed during the mid seventies, although the pattern is not as clear as it was with MDS.

If we consider now mean distances seasonally (Figure 46), the absolute difference between spring and fall MDS is usually small (approximately 5 nm) except for 1968, 1972 and the last years of data. During the early years of the fishery, MDS remained relatively constant at 20 nm from San Pedro for both seasons. This seasonal difference has no strong relation to either SB ($r = 0.34$) or harvest ($r = 0.33$) but as it was discussed in the previous section on distribution of harvest, for most of the period fall harvest takes place closer to San Pedro than spring harvest. There are large differences in 1968 and 1972 through 1974. However, after the peak abundance year of 1975 a switch was observed; spring harvest takes now place closer to San Pedro than fall harvest; and at the same time, both the overall MDS and the spring-fall difference increase. By the early 80's there were only a few schools spotted during the fall and these sightings were recorded at more than 40 nm from San Pedro; but by this time the fall anchovy fishery had ceased and the pilots were probably looking for other species.

The difference between both seasons is very small if we pool years during the

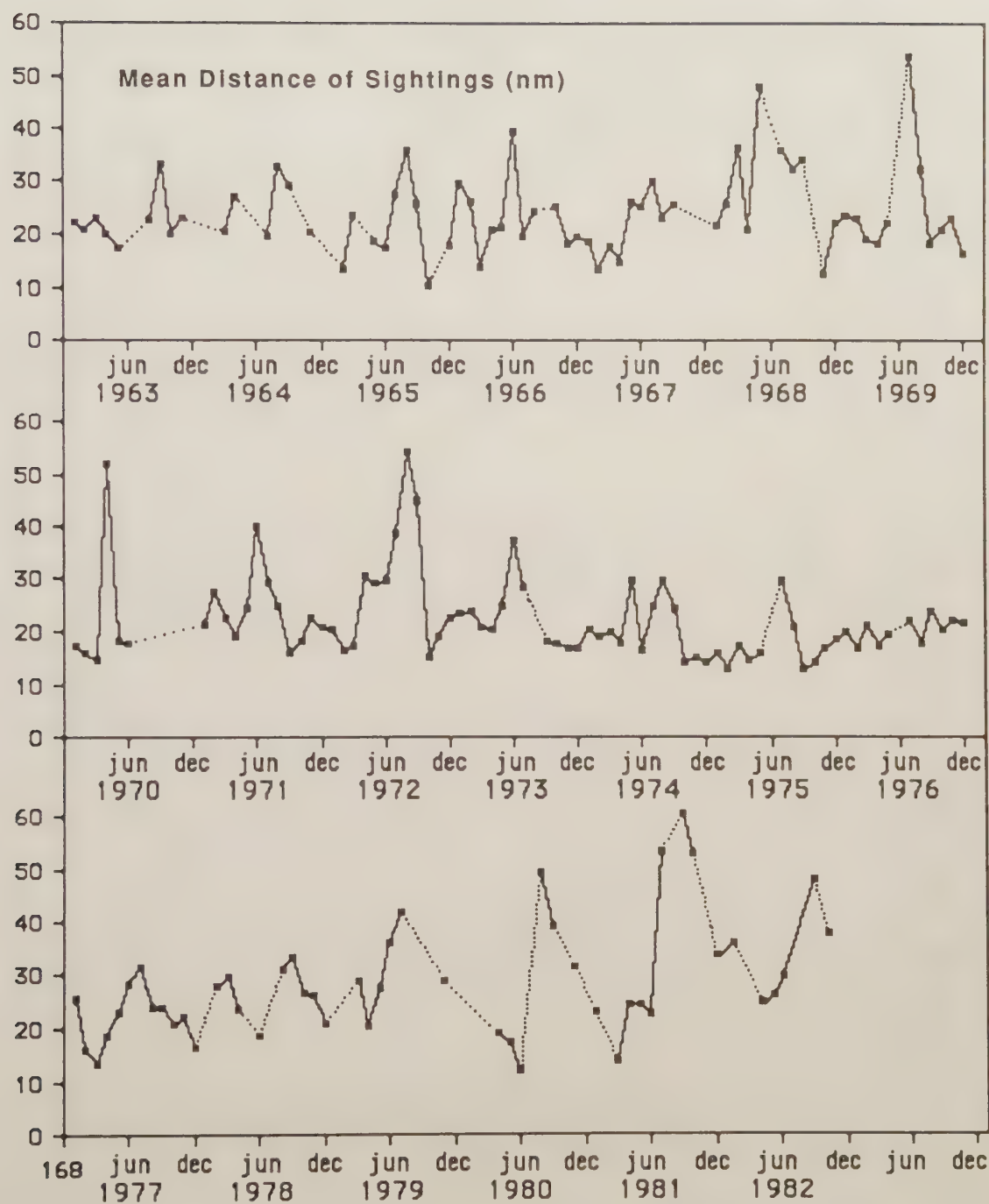


Figure 44. Mean Distance of Sightings by month, U.S. fleet. There is a general decrease in mean distance and its variability during the mid seventies. Data become sparse for the early eighties.

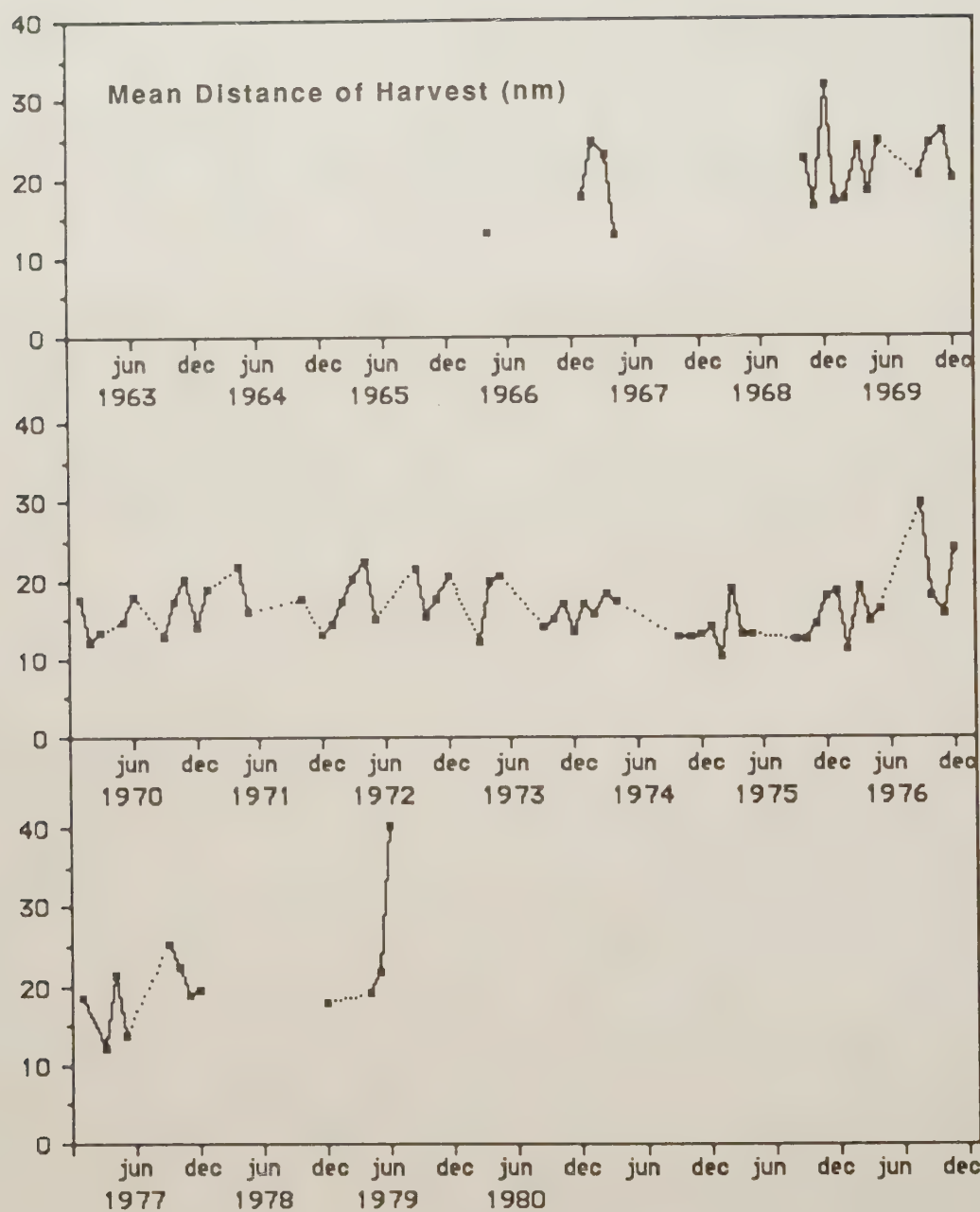


Figure 45. Mean Distance of Harvest by month, U.S. fleet. Data are more sparse than for the MDS series (see figure 44). In general, there is less variability in harvest than in sightings mean distance. The lowest values in MDH are recorded also during the mid seventies.

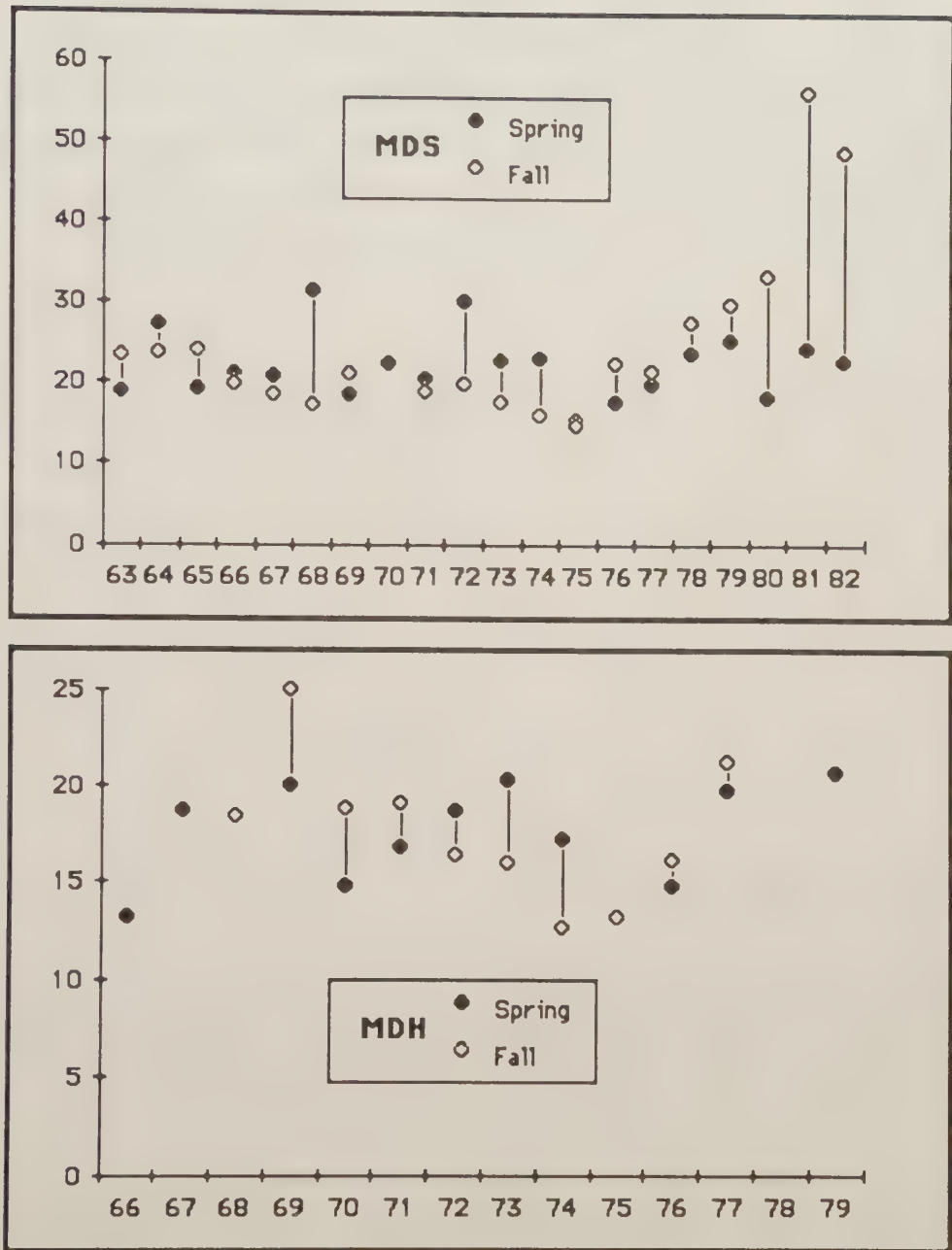


Figure 46. Seasonal difference in MDH and MDS, U.S. fleet. Until 1974 mean distance of sightings and harvest (nm) was higher during spring. After 1975, the year of highest anchovy abundance, both MDH and MDS were higher during the fall season. Lowest values and variation was observed during the mid seventies.

periods considered in the previous section on seasonal variation in the fishery (the periods are 1969-1973, 1974-1977 and 1978-1979). The general tendency of MDS to decrease with increased biomass is also apparent, particularly during the mid seventies and the subsequent increase during the late 70's and early 80's.

MDH by seasons data includes a smaller period, but in general the same pattern can be detected. During the early years of the fishery MDH was approximately constant at 17 nm; the lowest values were recorded during the mid 70's, with an increase during the early 80's. The reverse in spring and fall MDH after 1975 is not as clear as the change in MDS due to the lack of data (during 1978 the fishery almost ceased and there was no fall fishing during 1979). However, for several years prior to 1975 fall sets were closer to the fishing port, but after 1975 spring harvest was closer to San Pedro, following the pattern of MDS. The absolute difference between spring and fall is relatively constant (approximately 4 nm) until 1974 and declines the following years. In general, both MDS and MDH distributions mirror each other during the years 1972 to 1979.

Mexican Fleet

Correlation Coefficients

Table 10 shows the correlation matrix of coefficients among variables for all the Mexican data years. Coefficients in bold are significant at the 0.05 level; coefficients underlined are significant at the 0.1 level. The rest are not significant.

Spawning biomass (SB) does not seem to be strongly correlated to any of the variables considered, except for a slight correlation to landings (HARV) by the selected boats and for a significant relation (this was also true for the U.S. fleet, low biomass years, see Table 9) to catch per trip (CPTRIP). Despite the pattern observed on concentration rings, this may indicate that catch per trip for the Ensenada fleet could be used as an index of anchovy density when overall abundance is low. This is the case during the years considered, as spawning abundance did not surpass 700,000 tons. If fishing vessel carrying capacity is relatively low (as it is the case with

the U.S. fleet), CPTRIP could be expected to be constant and independent of SB (because a vessel can be filled after only one or two sets). However, if carrying capacity is large and SB is low, CPTRIP should be more related to SB.

Harvest by the Ensenada selected boats is also associated with the number of trips (NTRIP) and catch per trip (CPTRIP) as well as with the area harvested (in number of statistical blocks, BLOCK) and the harvest per statistical square (CPBLOCK). The relationship is high and positive for all these variables indicating again, that landings tend to be higher when trips concentrate in only a few places. This indicates also the tendency of the Mexican fleet to concentrate fishing activity in only 2 or 3 sites along the coast, as indicated by the gaps in NTRIP and harvest (see section on concentration rings).

As expected, mean distance of harvest (MDH) is related with the standard deviation of the distribution (SDDH) and with the variance to mean (VARMH) ratio. However, it is also associated with the area harvested, with CPTRIP and negatively with the number of trips per block (TRPBL). Thus, as the area fished increases the mean distance the boats travel and its relative dispersion also increase, as the fleet explores new fishing grounds far away from port. The negative correlation coefficient of MDH with TRPBL, and also with BLOCK and CPTRIP indicates that as the fleet travels far away from Ensenada, it tends also to make less trips to each block, concentrating its attention in only a few spots, as stated before. The relation to CPTRIP shows another tendency which is to harvest more per trip as the trips gets longer. This agrees in general with optimal foraging theory, and will be reviewed in detail in Chapter III. In the case of the Ensenada fleet, those boats with more autonomy (e.g. higher tonnage) are the ones which usually undertake the longest trips, contributing significantly to this association of CPTRIP and MDH. This is a significant difference with the U.S. fleet, where most boats have low carrying capacity. This pattern can be appreciated also in the highly significant relationship between the number of trips and CPBLOCK. As more trips are made during the fishing season, the catch per block also tends to increase because more and more trips are made to the same statistical areas .

Mean Distance and Biomass

As was the case with the San Pedro fleet, there seems to be no apparent relation

between MDH and spawning biomass for the Ensenada fleet (Figure 47). However, in the Mexican case the correlation coefficient is positive and not significant, while the relationship was negative for the U.S. data. At any rate, the significance of the estimate is too low to reject the null hypothesis of zero slope.

However there seems to be a negative tendency for all the years except 1980 which registered both the largest biomass and the largest mean distance (this might indicate that it is worthwhile for fishermen to explore when conditions are ideal; this of course is better than to explore when conditions are not as good) and 1982, when most schools were caught very near to Ensenada, particularly in the northern areas. As stated before, this may be a consequence of the 1982-1983 El Niño warm temperatures that drove many fish species north of their normal range. Thus the fleet concentrated in this region because there were no commercial concentrations in the south during these years.

The lower graph in Figure 47 is the scatterplot of SDDH and SB in which there is no statistical relation to biomass. All the points are very scattered, but it is important to notice that 1980 had again one of the largest dispersion estimates, while during 1982 and 1983 sets were made very closely spaced and mostly near the port.

Mean Distance over Time

A look at the data over the years 1978 to 1985 shows patterns that might help to explain some of the correlations (Figure 48). Spawning biomass has remained relatively low (below one million tons) during these years at an average of 500,000 tons with a minimum of 309,000 in 1984. MDH and SDDH are well correlated because they follow each other closely. There is a strong tendency to make more dispersed sets when the fleet travels more, but using only a few places close together when travel journeys are closer to Ensenada. It is interesting to notice that the lowest values of both variables occurred during El Niño of 1982 and 1983. Landings and number of trips sampled are also well correlated, because they show the same patterns: e.g. there is a decreasing tendency starting in 1982. Fishing activity during these two years was centered very close to the fishing port and concentrated mainly in the north of the fleet range (see harvest maps in section II) with only a few sets made near Punta Colonet. As expected, the same pattern can be observed in the total area fished. However, during 1984 the area exploited increased, with a consequent

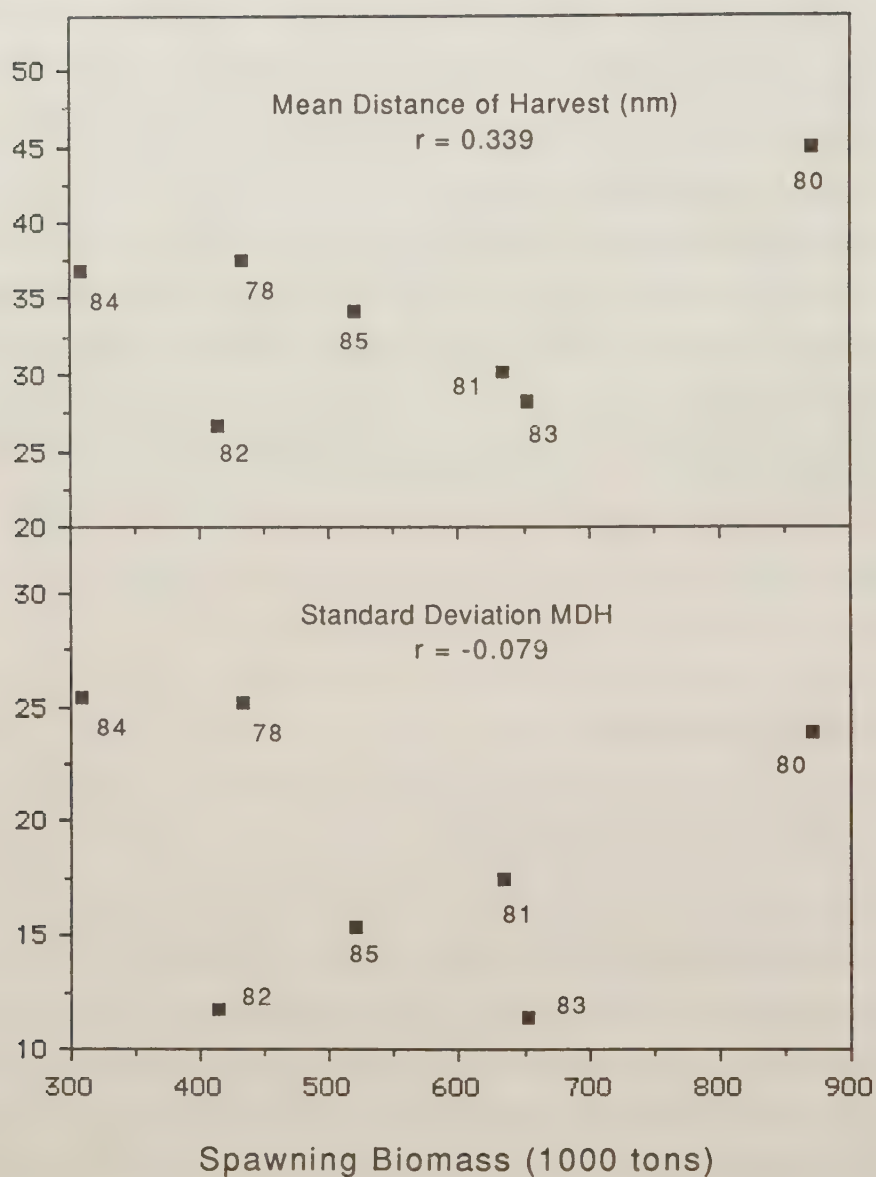


Figure 47. Mean Distance of Harvest and anchovy biomass, Mexican fishery. There is a positive correlation between MDH and biomass for the Mexican data, but it is strongly affected by only one year (1980). No relation is apparent for the standard deviation of MDH.

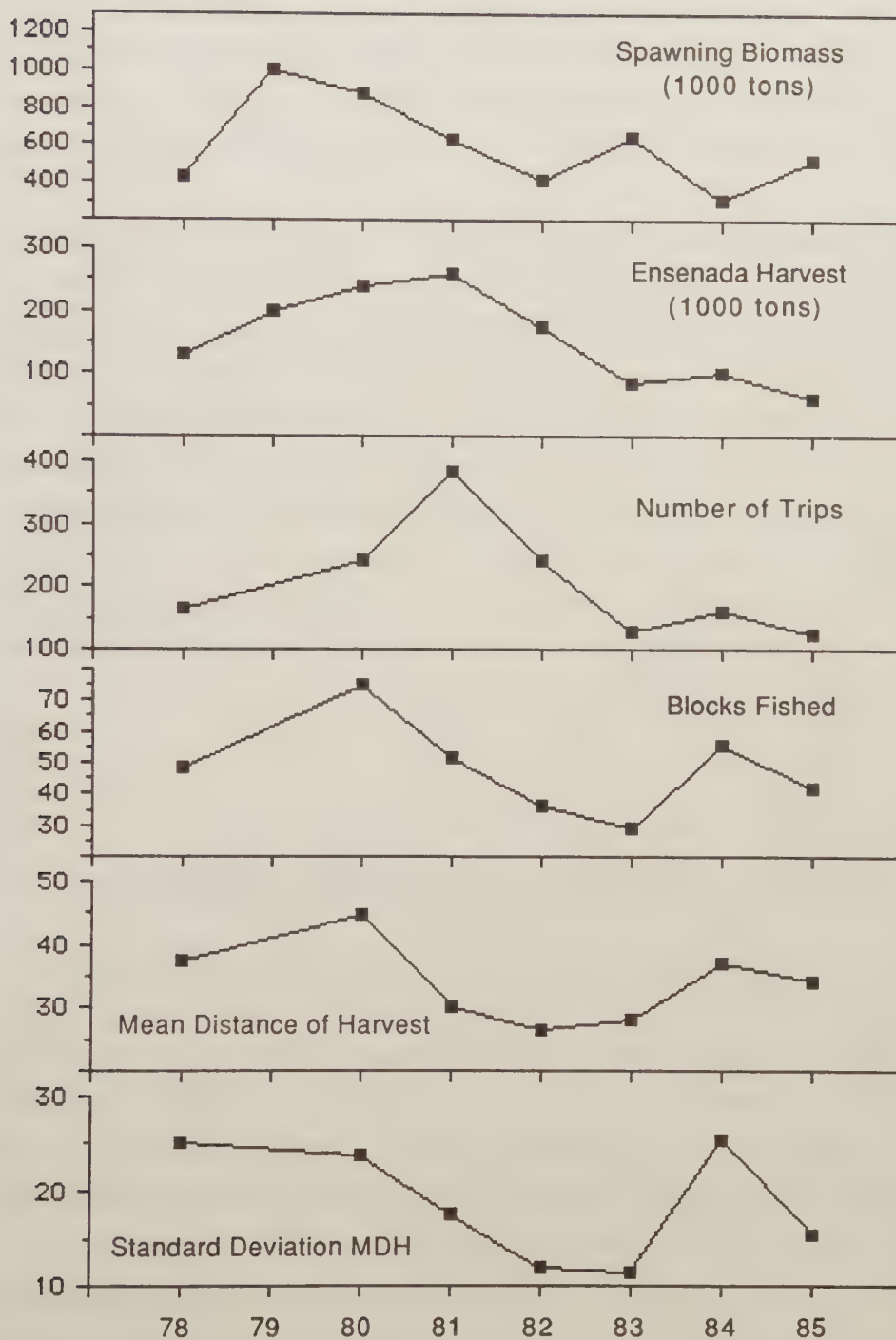


Figure 48. Mexican Fishery, 1978-1985. Area exploited (blocks fished) seems to be related to MDH and SDDH, while landings, trips and biomass follow somewhat similar trends.

increase in number of trips, landings and MDH and SDDH; but SB was at an all time low that period. The year 1985 shows a decrease in all the variables, particularly landings which were at an all time low despite a twofold increase in spawning biomass. It might be that these patterns are correlated to biomass the previous year, since most yearlings (age 0 fish) are not available to the fishery until the end of the year (late fall and winter). This certainly seems to be the case for the last few years of data.

Monthly mean distance of harvest by the Mexican fleet (Figure 49) shows high variability, with the largest peaks and variation occurring during the second half of 1980 and the early summer of 1984. The lowest points seem to occur during mid summer (except for 1984) at the height of the anchovy fishing season. As expected from the annual means and distribution maps, there is a decrease both in variability and in average values from 1981 to 1983, especially during El Niño 1982; as shown before, this phenomenon probably forced the fleet to fish the whole season mostly in the northern areas, at about 25 nm from Ensenada. The years 1978 and 1985 show also a low variability but the mean is somewhat higher than during 1982. However, there are no clear seasonal patterns, other than the tendency of the fleet to fish closer to Ensenada during the summer.

Mean Distance and Fishing Patterns

In relation to the first hypothesis (MDH decreases when SB increases), it does not seem that fishermen's location of fishing sets is strongly affected by changes in anchovy abundance above 920,000 tons; this seems to be true for both Mexican and U.S. fleets. The distribution of sightings however, is likely to be affected by the spawning biomass level. One possible explanation for this situation is that the U.S. fishing fleet has a much more reduced spatial domain of action when compared to that of the scouting airplanes (see Figures 20 and 26). The spatial domain of the scouting planes is also increased by the fact that pilots sometimes look offshore for other species, and report anchovy findings incidentally. This happens even during the fall and spring anchovy fishing seasons. Therefore, mean harvest distance for all years and sets is 17.55 nm (standard deviation = 3.18, maximum = 23.38, minimum = 13.18), located at the lower end of the sighting distance distribution overall mean

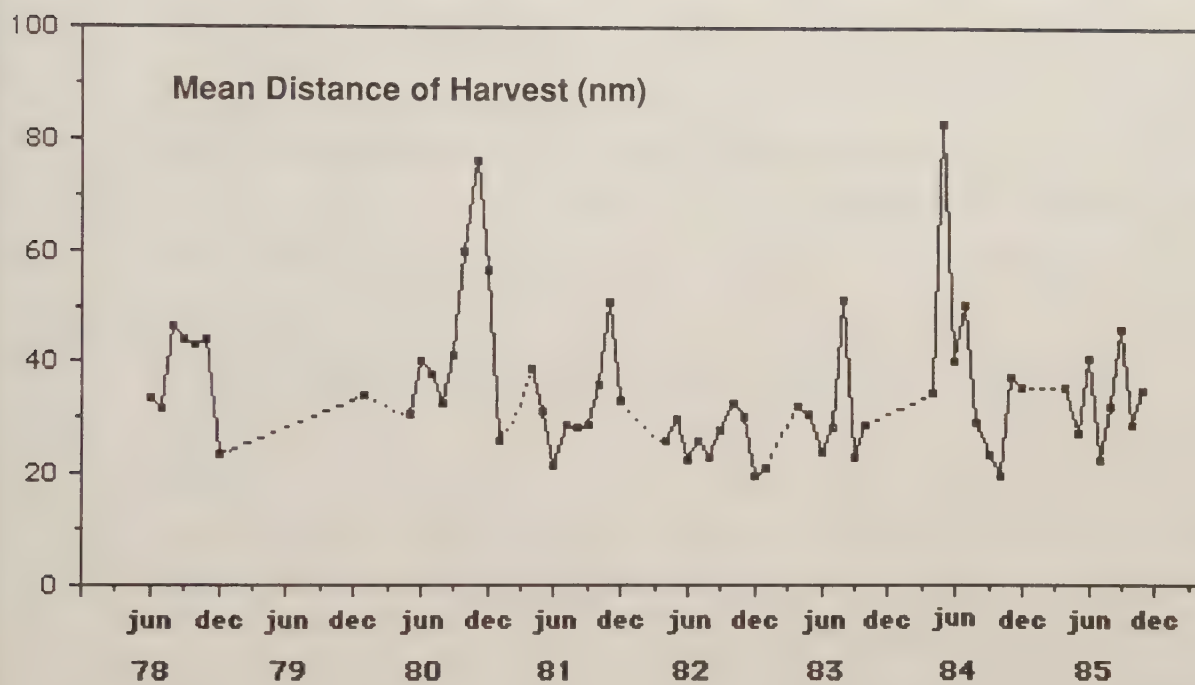


Figure 49. Mean Distance of Harvest by month, Mexican Fishery. No trends are evident for the monthly Mexican MDH data. However, two large peaks during 1980 and 1984, and a relative decrease in both MDH and variability during El Niño period (1982 and early 1983) can be distinguished.

20.49 nm (standard deviation = 3.16, maximum = 25.40, minimum = 14.86). This implies that although the spatial distribution of schools is probably changing with respect to spawning biomass - as indicated by the sighting distribution in Figure 20 - , these changes are relatively small within 18 nm from the fishing port which is the region more frequently used by the U.S. fishing fleet. Probably due to the spatially restricted range of the U.S. harvesting fleet MDH does not experience large changes with changes in anchovy abundance (e.g. school density does not vary widely in the area where the boats operate). On the other hand, the scouting airplanes are covering a much larger area, so that MDS may be more sensitive than MDH when measuring large scale changes in school spatial distribution and anchovy abundance. However, one important fact to consider is that the sighting distribution may be truncated after certain distance from the port because the pilots just don't look after a certain range. School density near the port is nevertheless usually higher for high abundance years than for low density periods (Figure 50).

As stated before, there are no sighting data for Mexican waters, but harvest distribution and MDH (Figure 47) information reviewed above seem to support the finds for the Mexican fleet, although no data are available for large spawning biomass (over one million tons) periods. The major difference is probably the scale over which the Mexican and U.S. fleet operate. Mexican boats seem to travel much more on the average to find suitable schools (overall MDH is 34.07 nm, standard deviation = 6.33, maximum = 44.83, minimum = 26.68), probably more due to the physical shape (e.g. no large Bay or islands as in Southern California) of the coastline than to the actual distribution of schools.

The overall situation is schematically depicted in Figure 51. Harvest takes place mostly from the center of the local distribution during high abundance years (51a) and to some extent from the periphery during low abundance years (51c). On the other hand, harvesting always from the center of the distribution implies that fishermen tend to overlook some schools which are near the fishing port. As this does not seem to be likely, the general strategy fishermen follow might be simply to harvest the closest desirable (in terms of school size) portion of the population (51b). However, it seems that boats don't travel more at low anchovy biomass, but they tend to make more dispersed sets. Notice that the variance of U.S. sets decreases with abundance for both sighting and harvest distributions. An interesting situation arises from this differential fishing effect upon the anchovy population: if there is a high viscosity condition (see Chapter I), fishing mortality will also be locally

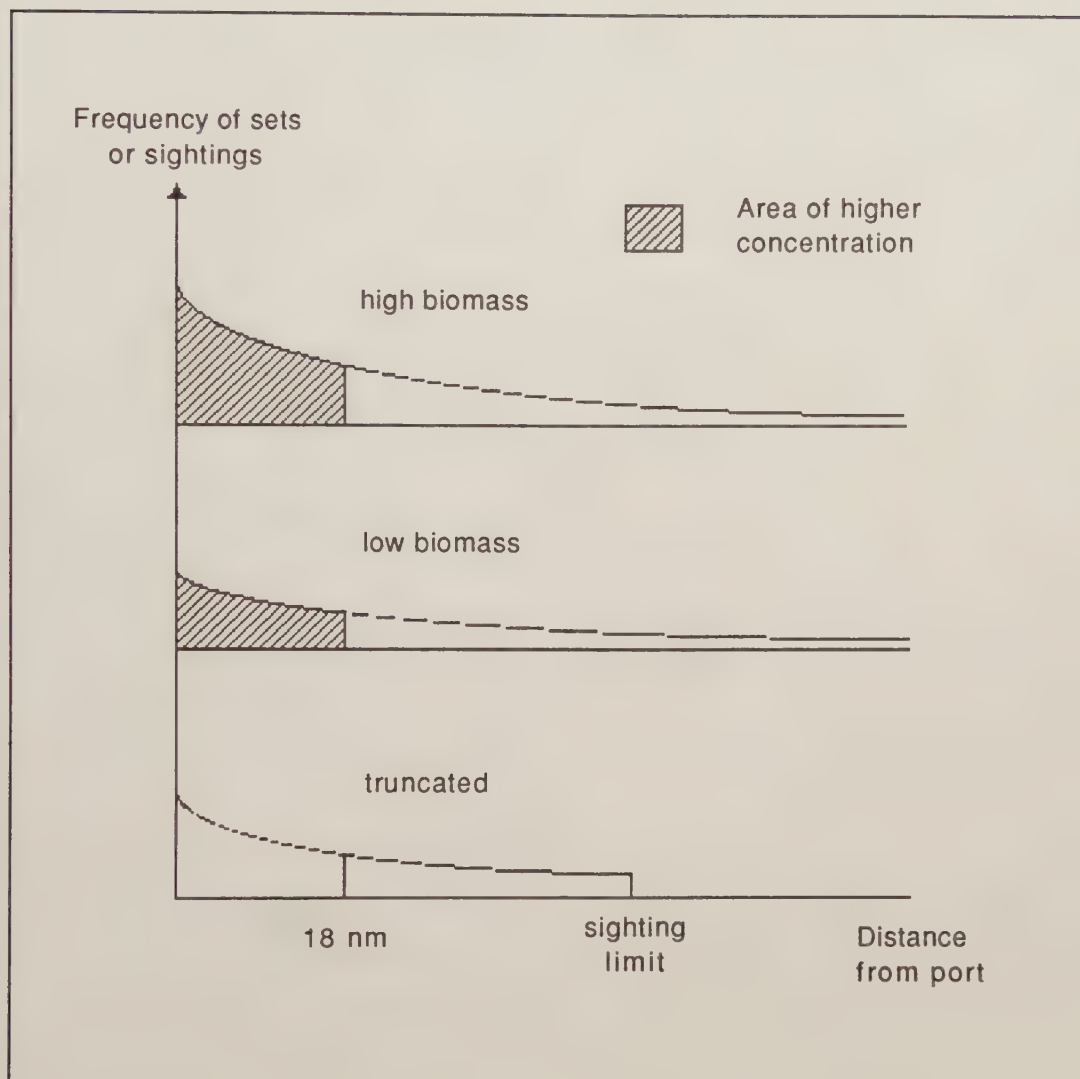


Figure 50. Truncated sighting distribution, U.S. fleet. The sighting function does not diminish asymptotically with distance. It probably ends abruptly at some point greater than 18 nm from port, because the pilots just don't look for schools any further. At all distances frequency of detection is higher for the high biomass years.

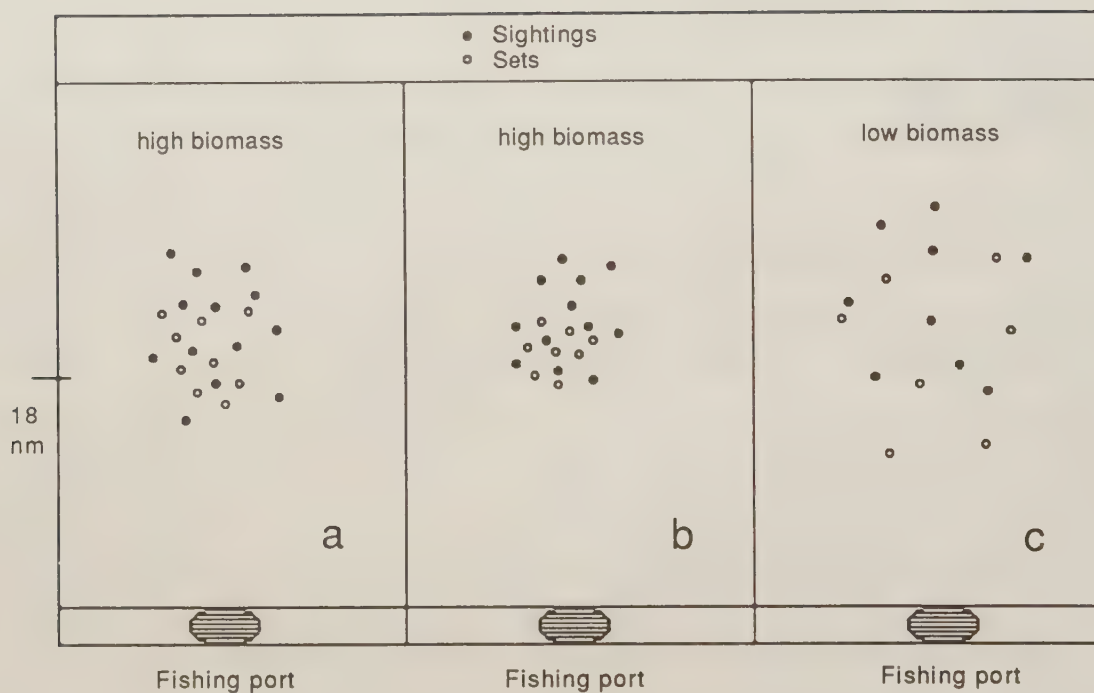


Figure 51. Relationship between sets and sightings, U.S. fleet. Harvest takes place from the center of the distribution when biomass is high (a). However, since fishermen do not overlook closer schools, the general strategy may be just to harvest the closest desirable schools (b). Landings come increasingly from the peripheral areas during low biomass periods (c).

variable, affecting some years more the peripheral areas which contain usually the older individuals and some years more the centrally located fish (see Figure 22 and 23, Chapter I). This differential effect will have undoubtedly some influence upon recruitment and the general dynamics of the anchovy population. The distribution of sightings and sets agrees in general with the density dependent theory of population distribution reviewed in Chapter I.

What can be said with respect to the second hypothesis ?. As we have seen, in general MDH is not equal to MDS for all levels of biomass in the U.S. fishery. Schools are consistently detected at slightly greater distances than those usually traveled by fishermen to harvest them. A regression between these two variables indicates that MDS has approximately a half unit change for one unit change in MDH, and this is significantly different from 1.0, the expected value if both distances are the same every year. The ratio MDS/MDH is therefore greater than one for most years (mean = 1.18, standard deviation = 0.1183) and its correlation coefficient to SB is relatively low and negative ($r = -0.339$, n.s.). This indicates a slight tendency of the ratio to decrease at higher abundances, probably due to the MDS decrease associated to high anchovy abundance. This tendency is particularly strong during years of low abundance. In fact, the correlation coefficient of the ratio and biomass changes to -0.742 when only low anchovy abundance years are considered.

As we have seen, MDS seems to change negatively with abundance, but MDH remains approximately constant, indicating that the fishing fleet spends most of its time at the same places, without this distribution being affected too much by abundance. This area is probably the closest one at which the right school can be found. As expected, both SDDS and SDDH decrease during years of high density due to the concentration of schools close to the fishing port. However, from this analysis alone it is not clear whether the schools are in fact closer to shore during high abundance years and more clumped as could be expected from density dependent habitat selection, or if the pilots just don't bother searching offshore, truncating the apparent distribution of local abundance of schools, producing the distributions of Figure 50. However, because SDDS is lower at high density, and due to the fact that the pilots search approximately the same area every year, it seems that anchovy schools tend to concentrate and to do so in the nearshore areas during high population abundance. The outer limits of the anchovy school distribution and its

influence over MDS and MDH however, remain unclear.

A look at the spatial distribution of aerial effort, sightings and sets during high (1975) and low (1972) anchovy biomass years in Southern California helps in clarifying this situation (see Figure 52). Although the area searched (e.g. aerial effort) by the aerial spotters is approximately the same both years, it is slightly larger during 1972, the low biomass year, particularly around the San Clemente and Santa Catalina Islands. Sightings are very concentrated in the San Pedro Channel during both years, but restricted to a smaller area in 1975, the high abundance year. Two 10' by 10' statistical areas near San Pedro account for most school sightings that year. The distribution of sets is very similar to the distribution of sightings but, as expected set/area are less numerous during 1972. However, during 1975 most sets were made near San Pedro, and as it was the case with sightings, harvest in a few areas accounts for most of the catch. The relation between sets and sightings per area is very strong both years (Figure 53), especially during 1975. MDS is higher than MDH probably due to the sightings associated with the offshore islands, while very seldom there are any anchovy sets recorded in that area.

From these maps and graphs, it seems that the aerial spotters search approximately the same area each year but they spend more time searching in the offshore region when biomass is low. Schools are usually concentrated in the nearshore area but they are less frequent when biomass is low and somewhat more scattered. The spatial distribution of sets is very similar, but during low abundance periods fishermen are willing to travel more to harvest the anchovy schools. This agrees in general with Density Dependent Habitat Selection (Chapter I); with Central Place Foraging Theory (the topic of Chapter III); and with the concentration rings phenomenon reviewed the previous section.

Factor Analysis

A factor analysis was performed for the U.S. data including the years 1967 through 1979 as before. Spawning biomass was excluded from the analysis, as many variables were associated to it, and it was one of the objectives to extract those factors related mostly to biological conditions. However, tons sighted per flight (TSIGFL),

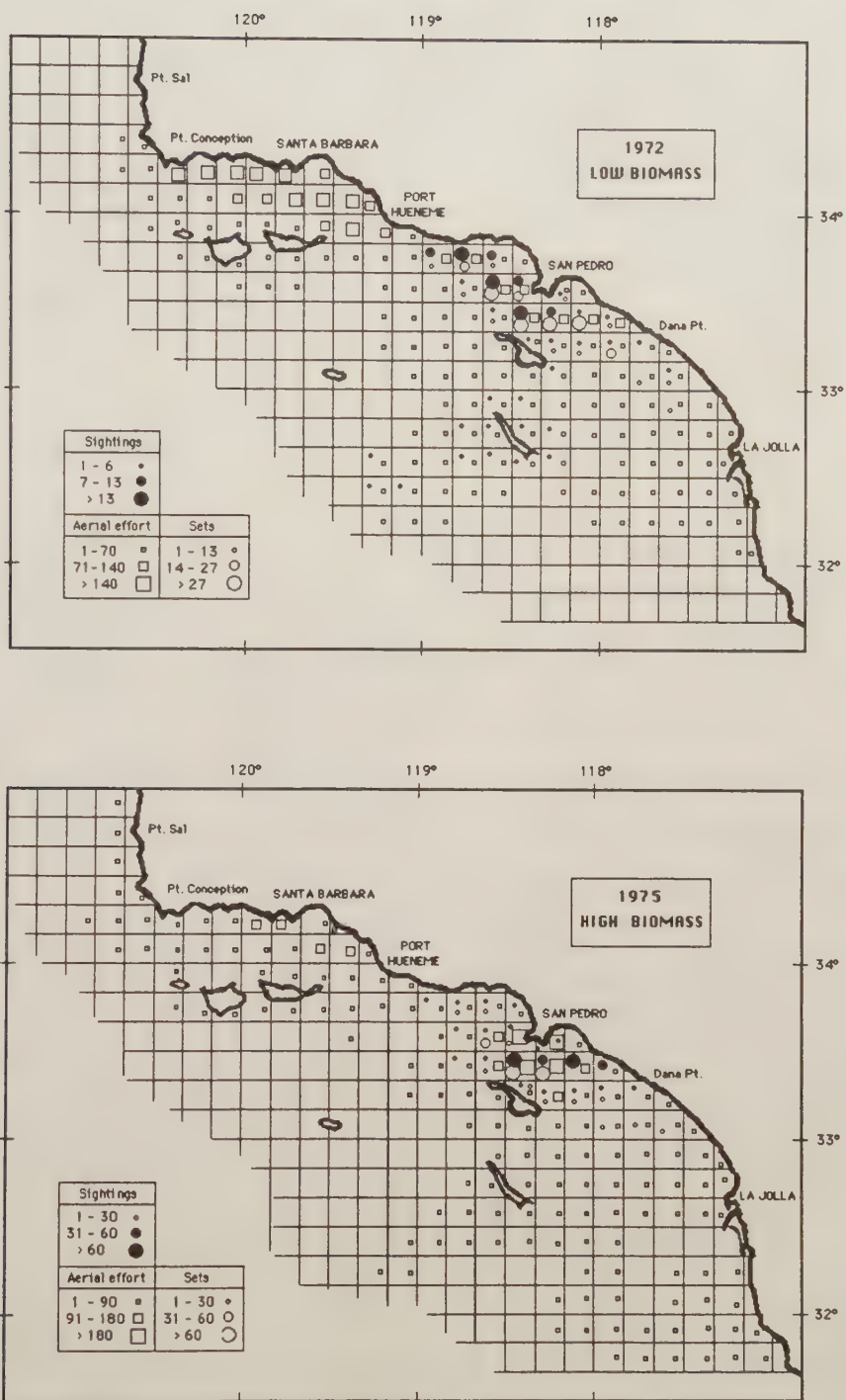


Figure 52. Harvest, sightings and aerial effort, high and low biomass. Two years are shown : 1972, low biomass and 1975, high biomass. Aerial effort is more extended in 1972, while sightings and harvest tend to be concentrated around the fishing port during 1975.

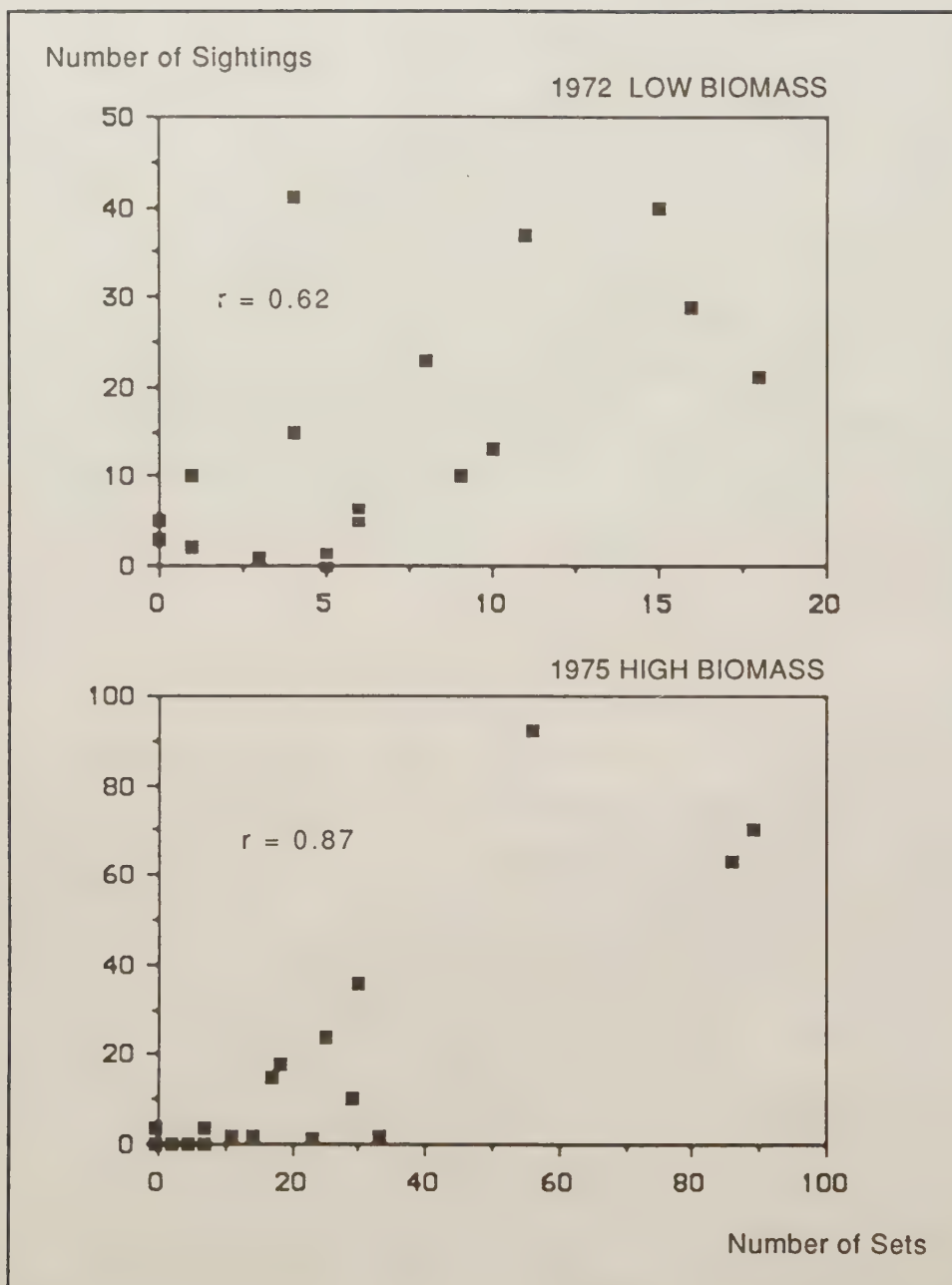


Figure 53. Sets and sightings for high and low biomass years, U.S. fleet. Each dot represents a statistical area. The correlation is high both years, although the scale is smaller during 1972. Three areas account for a large number of sets and sightings during 1975.

variance/mean of harvest (VARMH) and variance/mean sightings (VARMS) were included. Also, some of the economic measures, among them FMEALP (fish meal price per ton), FMIMP (amount of fish meal imported to the U.S.), ATONP (price per ton of anchovy in Southern California), as well as DIESEL (an index of diesel price) were considered because it was also expected that some of the factors would be related to a global economic variable such as revenue. The Mexican information was not considered in this analysis because there were only a few years of data, and no economic indicators were available.

Correlation Matrix

The first step in the analysis, the correlation matrix, shows the same relationships described before plus the correlation coefficient for the newly included variables. The relative abundance index derived from the sighting observations (TSIGFL) is related to CPTRIP ($r=0.640$ $p=0.021$) and to the price of diesel ($r=0.590$ $p=0.022$) which also affects CPSET ($r=0.500$ $p=0.049$). There is a tendency for the scouting pilots and fishermen to detect and capture more anchovy when the price of fish meal is high and/or when the cost of fuel is low. TSIGFL is also somewhat associated to SDDH ($r=0.449$ $p=0.071$) perhaps reflecting a higher average school size when the distribution is widespread during periods of high biomass.

The two variance/mean ratios are almost independent of the whole data set. As expected, the only significant correlations are with their respective standard deviations. If these variables are reflecting to some extent the degree of randomness of the set and sightings distributions, then this randomness of the spatial distribution is not strongly related to any other variable. Also as expected, the four economic variables are highly intercorrelated (all coefficients of correlation are greater than 0.624, $p < 0.015$). All the relationships are positive, except for fish meal imported which is negatively correlated to the rest of the indices. In addition, FMIMP is associated to SDDS ($r=0.736$ $p=0.003$) indicating that the pilots tend to expand their area of coverage when the anchovy price is high; also SIGH shows a negative coefficient ($r=-0.525$ $p=0.039$) with FMIMP, and a positive with FMEALP ($r=0.539$ $p=0.021$). Therefore less sightings are reported when the amount of fish meal imported is large. This indicates that the number of sightings may not only be reflecting anchovy distribution but also the willingness of the pilots to look for schools when market

conditions are ideal: since fish meal imports are national, the Southern California fishery can not fill the demand, so imports may increase slightly when the local fleet can not find enough fish.

Extraction

Five factors were determined using the extraction technique of principal components. Only those factors with an eigenvalue > 1.0 were considered for the rest of the analysis. The percentage of variation explained by the factors is as follows:

Factor	% Explained variation	Cumulative %
1	40.8	40.8
2	20.9	61.7
3	10.6	72.3
4	8.4	80.7
5	6.9	87.6

As can be seen, the first factor is very important, and the two first components account for more than 61% of the total variation. The first seven factors explain more than 96% of total variation.

The factor matrix showed that most variables loaded high in F1, at least four loaded high in F2 and several loaded high in both. Therefore it was decided to rotate the components to define new factors with clearer variable composition. Rotation was achieved by the VARIMAX (orthogonal rotation) and OBLIMIN (oblique rotation) methods, which yielded similar results, particularly for the first three factors which are the most important.

Table 11 shows variables assigned to each factor according to the ranking of their coefficients of correlation so that the largest coefficient of the variable SET is with factor 1, but SET is also the variable with the highest coefficient of correlation for that factor (a negative sign indicates a negative factor loading). As can be seen, the components are clearly separated for both methods of rotation and the results are very similar.

There are several variables that have a large coefficient for only one factor: SET, SIGH, and TRIP for F1; SDDH and VARMH for F2; ATONP for F3 and SDMDS for

Table 11. Variables ranked according to Factor Loadings. The first factor accounts for a large percentage of variation. Sets, harvest, trips and sightings are the most important variables

FACTOR % expl. var.	1 40.8	2 20.9	3 10.6	4 8.4	5 6.9
Varimax rotation					
*	SET HARV SIGH TRIP FMIMP FMEALP MDH	SDMDH VARMH MDH MDS TSIGFL CPTRIP -CPSET	ATONP DIESEL FMEALP -FMIMP TSIGFL -VARMS	SDMS VARMS MDS FMIMP MDH	CPSET CPTRIP TSIGFL DIESEL HARV
Oblimin (Pattern Matrix) rotation					
*	SET HARV TRIP SIGH FMEALP -FMIMP MDH	VARMH SDMDH MDH -CPSET TSIGFL MDS CPTRIP	-ATONP -DIESEL -FMEALP FMIMP -TSIGFL	CPTRIP CPSET TSIGFL	SDMDS VARMS MDS FMIMP MDH

* Variables in dark type have the highest value for that factor. The rest had also high loadings ($r > 0.300$).

F4. These variables can be considered “strong” in that component and tend to have also high weights for that factor. On the other hand, MDH, TSIGFL and FMIMP have a coefficient of correlation of at least 0.300 for 3 factors, so they are not very related to any one factor in particular. These “weak” variables also tend to have low factor weights.

The first factor is clearly separated from the rest and it is by far the most important, accounting for more than 40% of the total variation in the data. The most important variables in this component are all to some extent measuring effort. They are: number of sets, number of trips and number of sightings. Harvest by the seven boats sampled is also important, as it is related to the raw effort variables. FMIMP and FMEALP also load high in this component, as does MDH. An inspection of factor weights (see Table 12) shows in general the same patterns for factor 1, but HARVEST and DIESEL have a large influence in F1 due to their high weight. What can be said with respect to the first factor ?. The effort measures are indicating the willingness of fishermen to harvest and this is a good indicator of market conditions as reflected by the prices and the amount of fish meal imported to the U.S.. The factor is also dependent on revenue, as the diesel price affects directly the overall value of the fishery. There seems to be little of biological nature associated to this factor, but the number of sightings and to some extent the number of sets are dependent (as it was shown in the previous section) on abundance and density of schools. However school abundance does not seem to change drastically near the home port; therefore this factor alone could explain almost half of the variation in the data, that is, a good part of the fishery behavior (e.g. fishermen’s behavior) is shaped by market factors alone.

The second factor is also very important because it accounts for more than 20% of the data variability. F2 can be viewed as having a more biological (through school spatial distribution and density) interpretation, although it may also be influenced by economic conditions. The most important variables in this component are the degree of dispersion of schools captured (as measured by the standard deviation of the distance of harvest, SDDH), the mean distance of harvest MDH, and the variance to mean ratio VARMH, a rough indicator of the degree of randomness of the spatial distribution of sets. Thus, all three variables are related to some extent to the spatial distribution of schools, which is presumably driven mostly by biological-envi-

Table 12. Variables ranked according to Factor Weights. Factor 1, which includes sets, sightings and harvet is the most important; it accounts for more than 40% of total variation. Factor 2 accounts also for a large proportion of total variation (20.9%). See Table 11.

FACTOR % expl. var.	1 40.8	2 20.9	3 10.6	4 8.4	5 6.9
Varimax rotation					
*	SET HARV SIGH TRIP -DIESEL MDH	VARMH SDMDH -CPSET MDH TSIGFL CPTRIP	ATONP DIESEL FMEALP -CPTRIP MDS -FMIMP	VARMS SDMDS MDS VARMH MDH FMIMP	CPSET CPTRIP TSIGFL -ATONP -FMEALP DIESEL
Oblique rotation					
*	SET SIGH HARV DIESEL MDH TSIGFL	VARMH SDMDH CPSET VARMS SDMDS	ATONP DIESEL FMEALP CPTRIP MDS	CPSET CPTRIP TSIGFL -ATONP -FMEALP SET -SIGH	VARMDS SDMDS MDS MDH FMIMP VARMH FMEALP SET

* Variables in dark type have the highest value for that factor. The rest had also high weights.

mental forces (i.e. density dependent habitat selection; El Niño associated events). Also of importance for factor 2 are the rough indices of abundance CPSET, CPTRIP and TSIGFL. These patterns are in general duplicated in the factor weight matrix. Thus, this factor is probably representing the spatial distribution of schools caught, but the link to anchovy abundance is not very clear because MDH and the concentration rings from which it is derived are also the result of social and economic forces regulating central space utilization patterns. In addition, neither MDS (and associated measures) nor diesel price (and all the economic measures) are of importance to this component. Therefore, it seems that biological-oceanographical forces alone are driving a good proportion of the fishery, as expected.

The rest of the components are less important in terms of explained variation. All the economic indices: ATONP, DIESEL, FMEALP, and FMIMP are grouped in factor 3, which accounts for slightly more than 10 % of total variation. This factor is somewhat correlated to factor 1 when looking at the oblique rotation results. An inspection of the factor weights Table shows that CPTRIP and TSIGFL are also important for this component. Therefore, variation in foreign and domestic prices of anchovy and fish meal influence not only the number of sets, sightings and harvest (e.g. factor 1); but they are also related to these two CPUE indices, which to some extent might be measuring changes in anchovy abundance and availability. This again, is probably due to the disposition of scouting pilots and fishermen to travel more and to look harder for anchovy schools when market conditions are good; so that the changes in fish population density have probably a minor role in this pattern. Thus (as stated before), these CPUE indices might not be very reliable when measuring abundance.

Factors 4 and 5 are switched in order of importance when the loadings are rotated using the oblique technique, but they account for approximately the same amount of variability (8 %). Factor 4 is a component formed almost exclusively by the CPUE indices. As expected, this factor is also related to the price of anchovy, fishmeal and diesel. This reveals again that CPUE indices may not be a good indicator of abundance under spatial heterogeneity conditions, as they are influenced not only by biological but also by economic variability. Factor 5 is composed of the sighting distribution variables, the most important being the degree of dispersion of sightings and the degree of clumping of sighted schools. It is somewhat related to MDH

and to FMIMP, reflecting again the varying enthusiasm of scouting pilots to search for anchovy schools when economic conditions are ideal.

Factor Scores

Factor scores were computed (via regression) using the factor weights from the varimax rotation. The scores were also standardized and plotted against spawning biomass and revenue index. This index was calculated using landings and price per ton of anchovy and the index of diesel price. The resulting scattergrams are shown in Figures 54 and 55.

Spawning biomass has relatively high correlation coefficients with F1 (the effort factor), with F2 (the MDH factor) and with F5 (the CPUE factor). However, these relationships are not significant. For example, F1 and SB have a correlation coefficient of 0.38, but there is a single point (year 1973) which is driving up the slope. The regression seems to be slightly better against the MDH and the CPUE factors, as could be expected. On the other hand the revenue index has a strong correlation with the effort factor (F1) and a relatively high coefficient with F3, the economic measures component. The rest of the correlations are not significant.

Thus, the regressions give some support to the a priori hypothesized global components: one mostly related to economic forces and the other related predominantly to biological conditions. The first factor, the effort component, seems to be mostly driven by economics and it is the most important (40.8 % of explained variation). The second factor (the spatial distribution of harvest component) however, seems to be mostly influenced by biological variables and it is also very important (20.9 % of explained variation). F3, the economic indicators component is somewhat more related to economics while F5, the CPUE component, is more associated with biological measures. The position of F4, the distribution of sightings, is not clear in this context, as it does not have a significant relation to either revenue or spawning biomass.

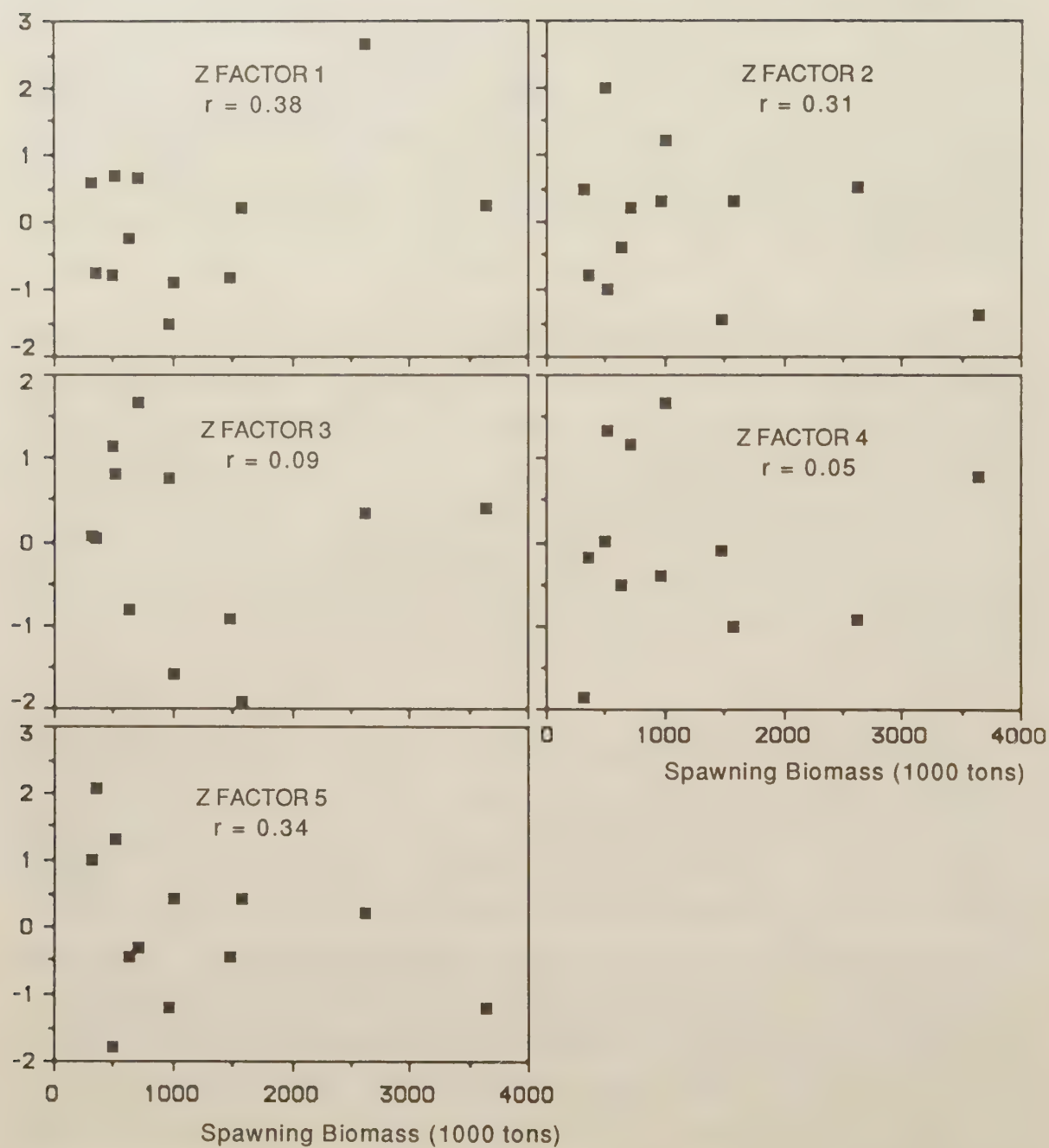


Figure 54. Factors and Spawning Biomass. No strong correlation is apparent. However, factors 1, 2, and 5 show a relatively high correlation coefficient.

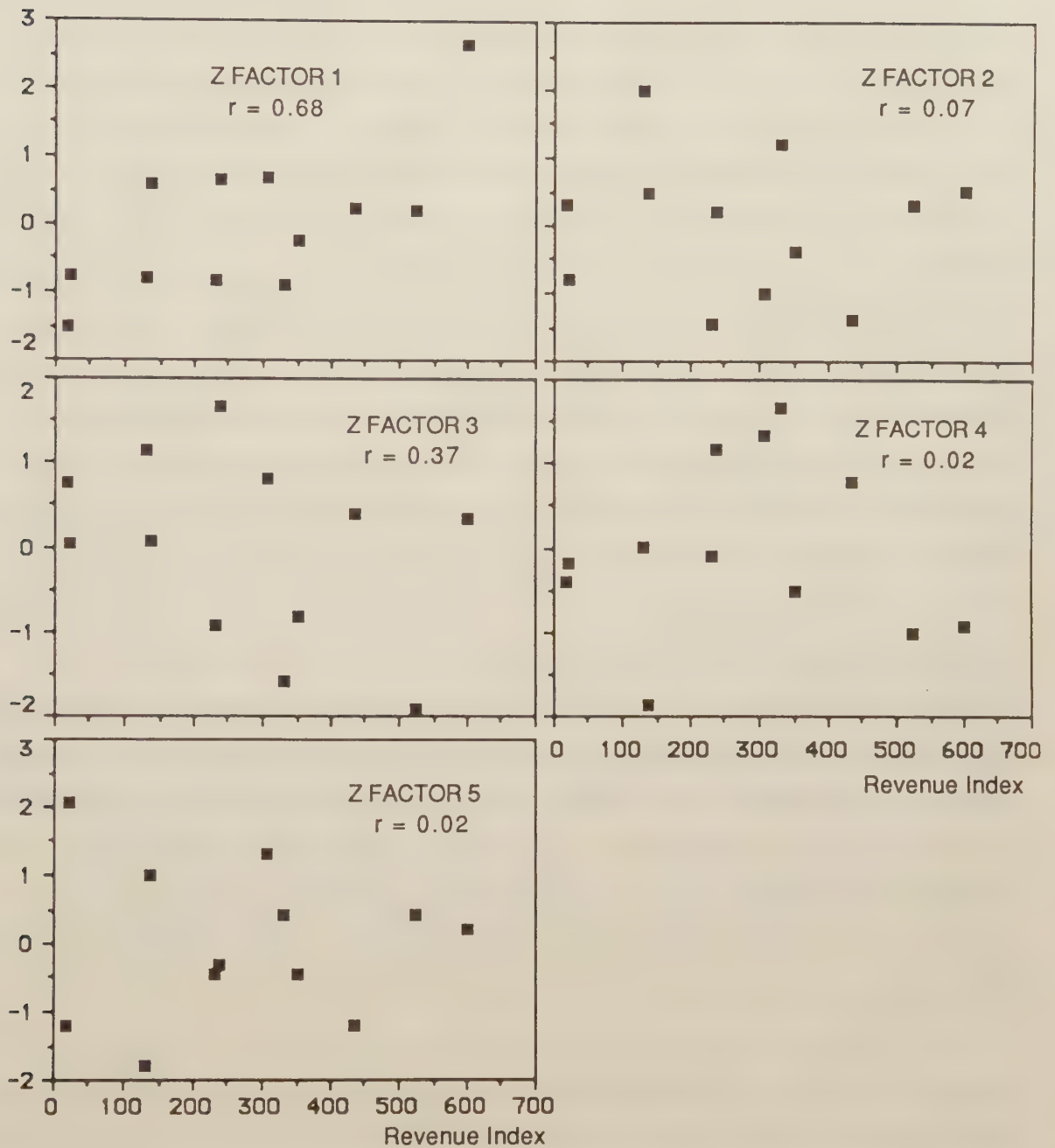


Figure 55. Factors and Revenue Index. There is a high correlation between the first factor and revenue index, and a relatively high relation with factor 3.

IV FINAL CONSIDERATIONS

As it has been shown, both the heterogeneity of the anchovy fishery and of the anchovy population are related to the extent that the distribution and abundance of schools in space and time determines in large part the distribution of fishing.

Temporal and spatial patterns have been described for both Mexican and U.S. boats. However, a direct comparison of the characteristics of both fleets has not been attempted. The reason is that although both fleets harvest basically the same resource, there are significant economic and social differences that affect the performance of each fleet. The U.S. fishermen have probably been fishing anchovy a longer time, but they are also more apt to be affected by changes in fishmeal and diesel price. In part as a consequence of this vulnerability, they have learned to switch relatively easily from one small pelagic fish target species to another; as it was shown, anchovy fishing has been a highly seasonal (spring and fall) activity. This is why during 1985 and 1986 anchovy fishing has been almost completely halted in Southern California, mostly as a result of market conditions. By contrast, the anchovy industry is relatively new in México but it has been much more stable, both socially and economically. In addition, it is almost a year-round activity and specializes mostly in harvesting anchovy.

Despite these differences, both fleets show similar space utilization patterns, particularly with respect to concentration rings around fishing ports. The explanation is probably related to the existence of constraints common to both fleets: a limited range of the fishing boats, the need of fresh catch for the processing plants; and the concentration of schools in the nearshore region. This situation forces fishermen to stay as close as possible to the fishing ports, producing characteristic distance-decay patterns of space utilization. The underlying nature of this situation will be theoretically explored in Chapter III.

Fishing fleet behavior can be conveniently summarized by the mean and the variance of the distance the boats travel to the actual site of capture of schools. Again, mean distance behavior patterns for both the Mexican and U.S. fishing fleets are similar. In particular, during high abundance years there is no simple relation between mean distance of harvest and spawning biomass levels. However, the factor analysis on mean distance and related quantities showed an influence of economic and biological components upon well defined groups of variables which exhibit similar behavior when compared to spawning biomass and an index of

revenue.

This chapter has established the local nature of the anchovy fishery (as the spatial and temporal distributions of aerial effort, sightings and harvest showed) for both Mexican and U.S. boats. It is not common for the vessels to capture schools at more than 60 miles from the home port. This regionality of the fishery is especially important when compared to the range and structure patterns (reviewed in Chapter I) of the northern anchovy population.

Fishing effects (e.g. fishing mortality) are probably higher in the nearshore environment, affecting only a small proportion of the population. However, this small fraction of the population is the one living mostly in the center of the distribution range, under the best conditions. Therefore, it can be assumed that contributes more to reproduction than the peripheral areas. Fishing has then a directional effect, selecting against the strong reproductive individuals within the stock. This is particularly important when taking into account that mixing is probably not complete within the population, contrary to what most conventional fishery management models assume.

This description has shown some aspects of the anchovy fleet dynamics, in particular boat movement. These patterns can not be ignored when considering alternatives for the management of fisheries of this kind. It has also been shown that fishermen respond to the spatial distribution of the resource, but they are highly influenced by economic factors as well.

Therefore, to comprehend the behavior of fisheries, it is necessary to understand the two basic components of a fishery system: on one side, the behavior of fish -the topic of Chapter I- and on the other, the behavior of fishermen; both empirically (issues described in this chapter) and theoretically (the subject of the next chapter)

CHAPTER III FISHERIES AND OPTIMAL FORAGING THEORY

I INTRODUCTION

Several authors, beginning with Emlen (1966) and McArthur and Pianka (1966) have tried to explain and predict the foraging behavior of animals using mathematical models. The models usually assume that natural selection will make an animal act as to maximize its fitness by improving its foraging efficiency, that is, by foraging in some optimal way. For example, natural selection will favor efficiency in hunting because a predator can improve its survival or reproductive success by improving the way in which it collects food. The “currency” used to measure this efficiency is usually energy. These models, which are based on very similar assumptions, have become known as Optimal Foraging Models, and the theory upon which they rely -the collection of rules and decisions an animal must presumably follow in order to harvest food efficiently- is known as Optimal Foraging Theory (OFT) (Pyke et al 1977, Stephens and Krebs, 1986).

Most OFT has been developed without taking into account space utilization patterns; but many predators do not consume their prey where they harvest them, rather they return to a central place where the prey items are stored or consumed, either by the hunter or its offspring. This case is known as Central Place Foraging (CPF, from Orians and Pearson 1979) and although it follows in general the same rules as OFT, it presents some interesting variations because of the explicit consideration of space utilization patterns. In fact, OFT could be considered a particular case of CPF in which traveling time to the central place is zero.

BASIC QUESTIONS IN OPTIMAL FORAGING

In general, the hypothesized foraging behavior is such that some quantity is maximized or minimized, and the procedure to find this theoretical optimum consists of three steps:

1) Choosing a “currency”.

This choice is always arbitrary and may depend upon the particular circumstances of each system, but it is almost always based on energy. The basic hypothesis is usually that the net rate of energy intake will be maximized (OFT case) or that the rate of delivery to the central place will be maximized (CPF case). There are, however, some other currencies that could be appropriated for a particular situation, for example to:

- Maximize the net rate of food intake while foraging.
- Maximize the rate of intake of some particular nutrient or component of diet.
- Minimize fluctuations in the rate of intake of total food or some specific nutrient.
- Maximize the minimum (“Maximin”) rate of intake of total food or some specific nutrient
- Maximize net intake over a long time period, such as a year or a season.

2) Choosing the appropriate cost-benefit function.

This step is related to the development of the constraints upon which the system must work. The cost-benefit function is the mathematically derived relationship between the diet of an animal and its rate of energy intake (or the currency being optimized).

3) Solving for the optimum

Once the cost-benefit functions have been maximized, what remains is to find the point or rule which makes the choice optimum for that particular currency and situation. This optimum will be found by determining the diet that maximizes or minimizes the currency selection subject to the various system constraints.

OFT has been developed along a series of general problems that animals face in order to harvest their food. The most common types of decisions which are likely to be made by actively foraging animals (Krebs, 1978), fall within the following basic choice problem categories:

a) Optimal Diet

The choices here are made with regard to the types of prey (food) which are eaten, including both quantitative and qualitative choices. The basic question in this respect is: How to select the proper prey ?

b) Optimal Patch

The choice here concerns the particular place in which to forage, that is, which type of patch to feed in. The basic question, analogous to the optimal diet question is: How to select the most adequate patch in which to forage ?

c) Optimal Time Allocation

The choices in this category deal with the conflicting uses of time and relate to the questions: How long to stay in a patch ?, Which clues should be used in order to leave and look for a new patch ?

d) Optimal Searching Path

The problems posed here to the forager include the selection of the optimal speed and search pattern in order to hunt efficiently, including the problem of when to revisit a previously harvested (and also probably depleted) patch.

OPTIMAL FORAGING AND FISHERY BEHAVIOR

Both OFT and CPF were partly developed by borrowing ideas from non-ecological fields such as Economics and Geography. Accordingly, the theory of optimal foraging has analogies in these areas, and its results can be readily applied to other inter-disciplinary situations.

One such case is the fishery system, in which fishermen act as predators of fish, following some rules to harvest efficiently (efficiency usually measured in some utilitarian form). Fishermen are also subject to several constraints (many economic; but also biological and social), and it can probably be assumed that they are optimizing, or at least trying to optimize (or achieve) some particular goal. In a

system like this, the quantity fishermen want to optimize is probably related in general to catch rates (in some cases such as the multispecies fishery the parameter under consideration may be directly the value of the harvest, that is, catch rate multiplied by price). Some relevant measures, parallel to those developed for the biological case might include to :

- Maximize the net rate of capture while fishing (OFT case).
- Maximize the rate of delivery of fish (i.e. tons per hour per trip) to the home fishing port (CPF case).
- Maximize rate of capture of some specific size/age or quality of fish.
- Minimize the fluctuations in capture rate of fish of some specific size/age or quality.
- Maximize the minimum ("Maximin") capture rate of fish of some specific size/age or quality.
- Maximize net catch over a long time period, such as a fishing season.

These currency measures are analogous to those developed for the OFT and assume that maximizing capture rates will somehow increase fishermen's "fitness" (the equivalent of biological fitness can be thought of in terms of overall wealth), in a similar way as to the situation in which increasing the rate of delivery or the energy intake presumably increases Darwinian fitness for hunting animals.

The strategy which will produce an optimum will be based on certain "diet" in terms of number of fish or schools caught that maximize or minimize the currency or goal selected, and the outcome will also be determined (as it is the case with OFT) by the currency and constraints chosen. Therefore it is very important to carefully select the currency constraints according to the characteristics of the system under study.

Following the concepts stated above, the objective of this Chapter is to review briefly some of the results of OFT, with particular attention devoted to the Central Place Foraging case, and to discuss some of its applications and analogies to a fishery situation and its implications for management of fisheries resources. The specific

system under consideration is the northern anchovy fishery (*Engraulis mordax*), harvested by both México (Baja California) and the U.S. (Southern California). Most of the analysis will be concentrated on the general problems of selecting the optimal diet for both OFT and CPF, and of choosing the optimal patch in the case of CPF.

II OPTIMAL FORAGING THEORY (OFT)

OPTIMAL DIET MODEL

According to OFT, any prey item eaten has a cost in terms of the time taken to subdue and eat the item, and a benefit in terms of its net food value (net value is the gross value minus the energy costs of handling and digesting the food). The net value divided by the handling time is a measure of the profitability of a prey type. One basic assumption of this commonly stated OFT hypothesis is that prey items should not be taken due to conspicuousness, palatability or nutrient quality (Krebs 1978).

The maximization process is achieved by ranking prey according to their profitability (C/h_i), that is, their expected net energy content (C) divided by expected handling time (h_i). Therefore, a prerequisite for this model is that by sampling, predators are able to distinguish among individual prey items and to rank them according to their expected profit.

Several empirical studies have shown that in general these statements are true. For example, Elner and Hughes (1978) found that shore crabs prefer a specific size class of mussels to feed upon, and Davies (1977), showed that some birds, e.g. pied wagtails prefer and select certain size classes of flies. These studies have found that the available and harvested distributions of prey size classes are significantly different.

While it is intuitively easy to see why a predator should prefer a highly profitable prey, the question of to which extent a less profitable item should be included in the diet is not so obvious. A predator which is very selective will have a high rate of food

intake; but a large cost in terms of searching time. A non selective one will experience the opposite effect, so in order to achieve the optimum (Krebs 1978) there should be a balance between these two extreme strategies. In order to accomplish this equilibrium, the only prey types included in the optimal set are those whose profitability (C/h_i) is greater than the expected rate of energy intake if the prey were not consumed, and the predator sought only prey with higher C/h_i . The predator expands its optimal diet to include lower ranking types when higher ranked items are hard to find, and contracts the diet in good environments (e.g. when higher ranked items are abundant). An important corollary of the theory is that whether a lower ranking prey item should be consumed is independent of its abundance, and depends solely on the abundance of higher ranked prey types. This implies that a certain prey type should not be eaten, no matter how common it is, as long as its C/h_i is lower than the expected rate of energy intake that could be achieved from a diet that does not include this prey type. Three important points derived from the above are that predators should :

- a) Prefer more profitable prey types.
- b) Be more selective when profitable prey are common.
- c) Ignore unprofitable prey which are outside the optimal set regardless of how common they are.

This is the commonly accepted theory in optimal diets, and was in part first proposed by MacArthur and Pianka (1966), and expanded independently by several authors. Proofs and detailed information can be found in Charnov (1976), Schoener (1971), MacArthur (1972), Pearson (1974,1976), and Pulliam (1974). General reviews of OFT have been written by Pyke et al (1977), Krebs (1978) and Krebs et al (1983). A recent discussion and references on general foraging theory can be found in Stephens and Krebs (1986). A treatment of the problem from a different point of view is that by Glasser (1984a), under which the resource values have an extrinsic component and the foraging behavior varies according to the environment and to the specialized or generalized nature of the consumers. Discussions of the usefulness of the optimality approach and the problems of finding appropriate currencies for behavioral responses can be found in Glasser (1984b), Jamieson (1986), McNamara and Houston (1986) and Stephens and Krebs (1986).

OFT and a Fishery System

As was stated before, many of the above ideas in optimal diet or “prey models” (Stephens and Krebs 1986) can be applied to a fishery system, since the fisherman is after all a human predator; perhaps not always making the most rational choice, but almost always trying to optimize some particular currency or to achieve a particular goal subject to economic, social and biological constraints.

If one considers certain pelagic coastal fisheries, one analogy is to look at individual fish schools as prey, and to view different school sizes (in number of fish, surface area or tonnage) as prey types, in the same way size classes of prey have been considered to be distinct prey types. Thus, an individual school harvested has a cost in terms of time necessary for searching, pursuing and handling it (h_j), and a benefit (S) in terms of its net value (gross value of tonnage minus the costs associated with fuel consumption, equipment, etc). The net value divided by the time is a measure of profitability of a school type (S/h_j). The predictions developed previously can be readily adapted to this system, so that it can be assumed that fisherman should :

- a) Prefer more profitable schools.
- b) Be more selective when profitable schools are common.
- c) Ignore unprofitable schools that are outside the optimal set (“optimal diet”), regardless of how common they are.

Thus, fishermen should take only those schools that are “worthwhile” to them, that is, only those that will produce the higher profit, so that the proportions of school types (e.g. proportion of school sizes) caught may be different from the proportions of school types available.

For example, during hydroacoustic surveys of pelagic schooling fish in the California Current, Mais (1974) found that the vast majority of schools observed were small. The author observed a total of 22,843 schools between 1966 and 1971. Although he found the area (surface m^2) of a school not very reliable as an indicator of total biomass, up to 75% of all daytime schools detected were less than 30 m in diameter (schools with a diameter greater than 40 m were exceedingly rare),

presumably of low tonnage as well. This pattern was consistently observed both in Southern California and in northern Baja California. During the same period however, commercial fishermen generally attempted to capture only schools of 20 tons or larger (i.e see Figure 36 Chapter II on concentration rings of catch per set). This size class constitutes a very small proportion of the anchovy school "population", and the average school size was much smaller than that; for the 1972 season, the estimate of mean school biomass was between 7 and 9 tons. Furthermore, Mais considers that a good estimate of mean commercial school size for the Southern California anchovy fleet is around 36 tons, and capture of schools 80 or 90 tons is not unusual. However, due to the individual schools breaking up and aggregating again, large captures may take place at different times of the 24 hour cycle.

This result clearly shows that fishermen capture only those schools which will produce a higher profit, so that the proportions of school sizes caught -usually quite large-, are very different from the proportions of schools available, usually small.

One problem with this approach is that anchovy fishing is generally a night operation; but the acoustic surveys are carried out during the day, and it is not known to what extent schools break up at night and reorganize in the morning. Nevertheless, the evidence reveals a peak indicating Southern California fishermen's preference for a particular school size or type.

Optimal breadth of diet (e.g. number of school types in the optimal set) depends on school size availability, and this can be shown graphically combining the searching time (assumed inversely proportional to abundance) and profitability (Figure 56). This graphic model is an adaptation of the original model proposed by MacArthur and Pianka (1966).

The graph shows how both travel time and average profitability decrease with increased breadth of "diet". Travel time, assumed to be inversely proportional to school density, falls off more rapidly than the curve of average profitability, based upon the assumption of a normal distribution of school profitabilities.

As more school types (e.g school sizes) are aggregated to the optimal set, the travel time diminishes, but so does the curve of average profitability of school taken. Therefore, the curve of profitability per school per time searching increases up to a peak and then declines sharply. This peak shows the optimal number of school types

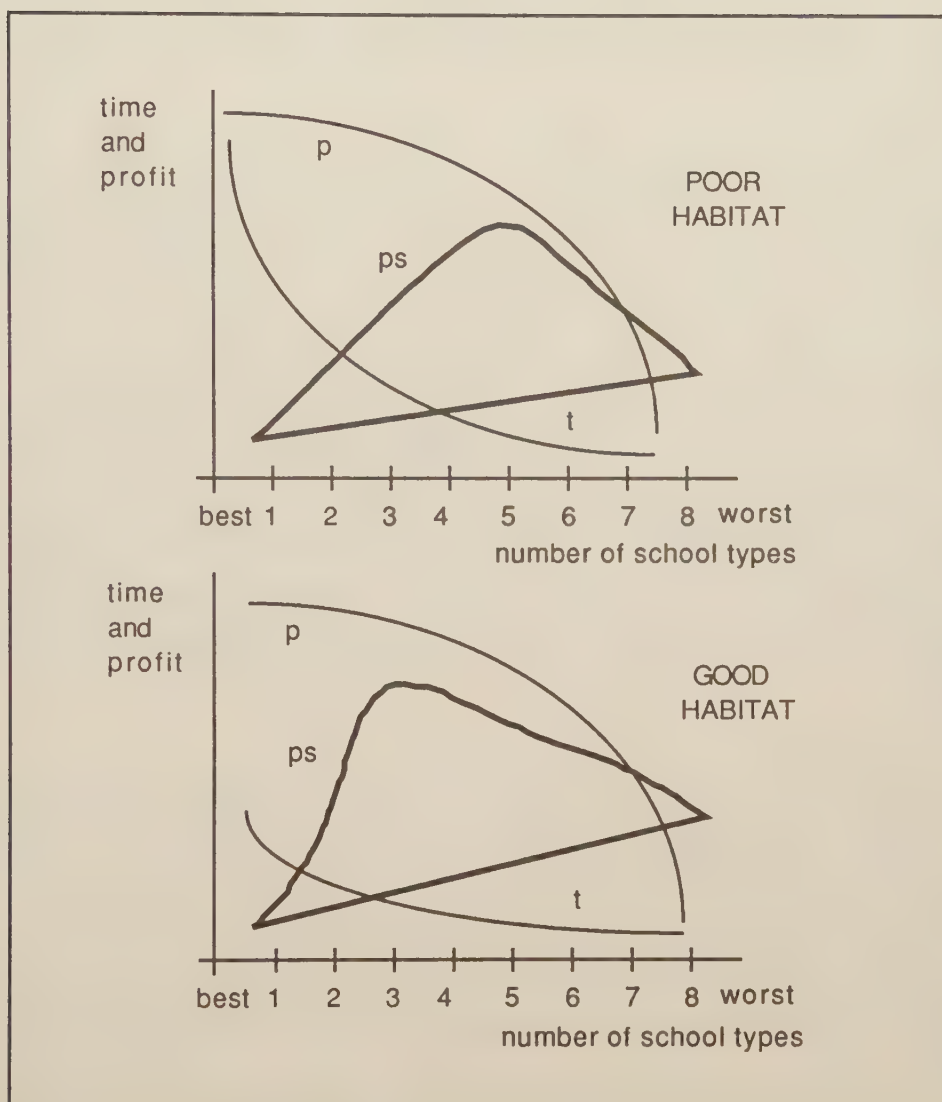


Figure 56. Number of school types in optimal set. Number of school types in the optimal set (peak of curve ps) is low in the good environment. In the upper curve, the optimal set should include five school types. In the lower curve, the more favorable environment, the optimal set consists of only three school types. Prey items are ranked in order of profitability. t = travel time; p = average profitability of school type; ps = profitability per school per unit searching time. Adapted from MacArthur and Pianka (1966).

in the optimal set. In the poor habitat where high-ranked school types (e.g. large sizes) are scarce and travel time is large, the peak includes more school types. The graphs show that the combination of profitability and travel times gives the optimal number of school types and if the availability of higher-ranked schools increases, the optimal set includes fewer types because the travel time for the selective fisherman is shorter.

This is equivalent to saying that in a habitat where high-ranking schools are abundant, it is not worthwhile for a fisherman to go after a small school that has low profitability. This point can be illustrated in Figure 57 in which the fishermen's current rate of school intake (including traveling time) is shown as the slope of a thick line, and the profitability of two new school types as the slope of two narrow lines. Fishermen should not take any school type A, because its profitability is below the thick line. The reverse is true for schools type B, since fishermen will clearly benefit from taking this school. The point is that type A should never be taken because its profitability is lower than what can be achieved from a set of school types that does not include type A. This is true even if schools of type A are very common, since the slope of the solid line cannot be increased by adding these schools to the optimal set.

One problem with this graphic model in the case of the southern California anchovy fishery is the limit on landings (discussed in Chapter II) imposed by canneries. Due to this restriction, a fisherman may fill up his allowed vessel capacity in just one or two sets. One implication of this limit is that there may be only two types of school to the fisherman: those above and those below cannery limits, reducing the effective number of possible prey types in the diet to only two.

The main point of this model is that optimal breadth of diet depends only on availability of profitable (e.g. large) schools, and this implies that:

- 1) The lower-ranked schools (e.g. low biomass) should be dropped from the optimal set at high density of good schools.
- 2) Lower ranked schools should never be included in the optimal set, no matter how abundant they are.

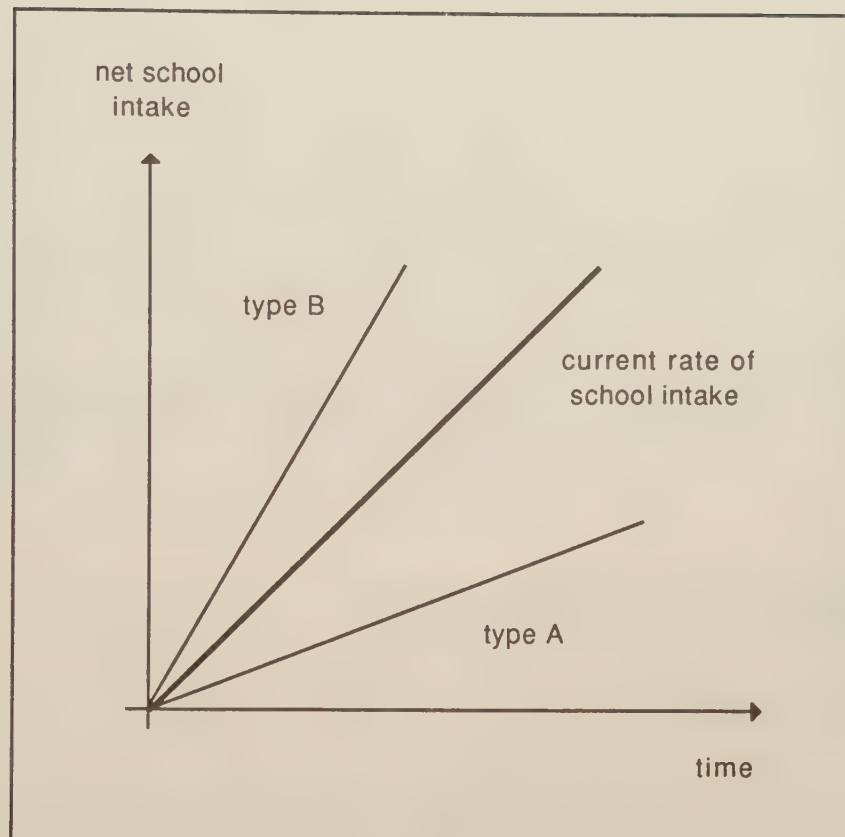


Figure 57. Relative school profitability. Fishermen should never take schools type A, no matter how abundant they are, because the current rate of intake for that area is higher. Conversely, schools type B should be taken whenever found, since their profitability is higher than the current rate of intake. Adapted from MacArthur and Pianka (1966).

These ideas imply that fishermen should take school types in the same frequencies as they are found in the fishing grounds when large schools are scarce. When density of highly profitable schools increases, fishermen should be increasingly selective, dropping small schools from the optimal set (Figure 58). The upper set of histograms in the Figure describe the ratio of encounter rates (based on searching time) with each school size class at three different densities. The medium row of histograms show the prediction from OFT: at medium densities, small schools should not be captured while at high densities both medium and small schools should be ignored. The lower row of histograms shows a probable outcome : although medium and small schools should be ignored at high densities, it is likely they will be captured occasionally. This difference between prey type available and taken at varying prey densities has been observed in many species i.e. Werner and Hall (1974) bluegill sunfish experiment and Elner and Hughes (1978) study on shore crabs. This difference between prey type available and taken at varying prey densities has been observed in many species i.e. Elner and Hughes (1978) study on shore crabs.

III CENTRAL PLACE FORAGING (CPF)

OPTIMAL DIET MODEL

If we consider now these optimal diet models but in a situation in which a predator must return to deliver the prey to a central place, we need to explicitly take into account travel time. The basic unit in CPF is the round trip (Orians and Pearson 1979), composed of an outbound trip, a foraging period and a return trip. Energy is expended in all three phases of the trip; but it is acquired only during the actual foraging. Also, the return trip -all other things being equal- should cost somewhat more to the predator since it is carrying an extra load of prey.

In the CPF case, as in OFT, every individual prey has a cost in terms of time taken to subdue and eat the item, plus a cost in terms of the round trip necessary time for being in the right patch to attempt the capture. Therefore, profitability should include now a roundtrip component. The currency which is assumed to be maxi-

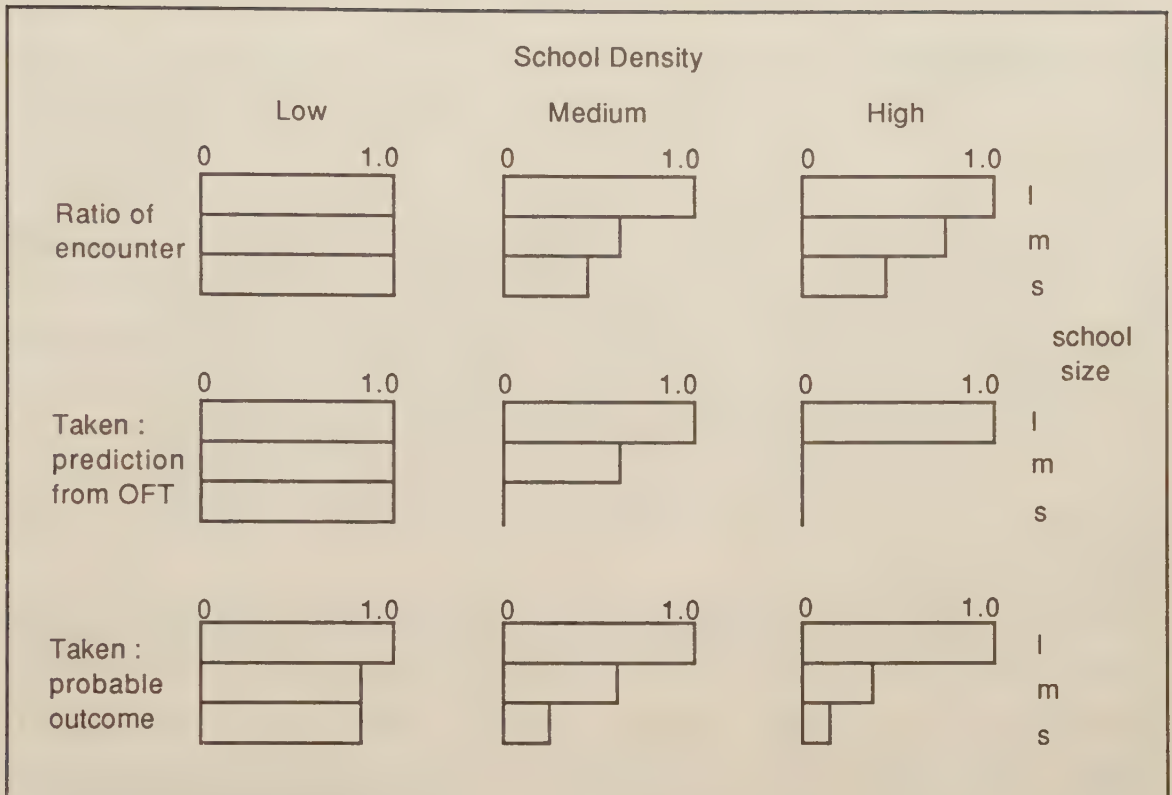


Figure 58. Ratio of schools taken at varying densities. Fishermen should be increasingly selective at high densities of desirable schools; in this theoretical situation they should drop small schools from the "optimal set". The histograms show ratio of encounter rates (e.g. searching time) with each size class at three different school densities together with predicted (from OFT principles) fishing rates and a probable outcome, where small schools are not likely to be dropped completely from the optimal set. l = large schools; m = medium schools; s = small schools. Based on Werner and Hall (1974) experimental bluegill sunfish study.

mized in this situation is the rate of delivery of energy to the central place, and the optimization is again achieved by ranking preys according to their profitability. In this context, profitability ($C/(h_i+T_i)$) is now the energy content (C), divided by the sum of expected handling and roundtrip times (h_i+T_i).

The general results of CPF indicate that as distance, and hence traveling time from patch to central place increases, the larger should be the prey energy selected. In addition, within a patch, the same criteria already developed for non CPF applies, that is, if each prey type has associated a fixed energy and a fixed time expenditure, the optimization is achieved by ranking the i th prey according to its $C_i/(h_{ui}+T_i)$, so that the same prey may be ranked differently in patches situated at different distances from the central place. For short traveling times, the superiority of a prey depends on its energy per unit handling time; but for long traveling times, the handling time becomes less important and the value of a prey depends mostly on its energy content. The actual diet in a patch should depend only (as it does in general OFT) on the availability of high-ranked types, and the predator should be more selective when in good environments; poor situations (low abundance of high ranked prey types), should produce a broadening of the optimal set to include some of the lower-ranked items.

This is the general single-loading CPF concept as proposed originally by Orians and Pearson (1979). The theory has been modified and extended to include particular cases by several authors, including Martindale (1982), Lessells and Stephens (1983), Houston and McNamara (1985) and Ydenberg *et al* (1986). Tests of some of the models (mostly on birds, as the theory was first proposed in an ornithological context) can be found in Kramer and Nowell (1980), Carlson and Moreno (1981), Carlson (1982), Bryant and Turner (1982), Brooke (1983), Hegner (1983), Kacelnik (1984) and Houston (1985).

CPF and a Fishery System

Using appropriate analogies, most of these ideas can be readily applied to fisheries, as was done for the non CPF case. Schools should now be ranked according to their profitability ($S/(T_s+T_i)$), that is, the school net value (S) divided by the sum

of expected searching (if we consider handling time negligible) and traveling times ($T_s + T_t$). The treatment that follows is an adaptation of some of Orians and Pearson's (1979) models, in which the following assumptions are made:

- 1) The predator can search simultaneously for prey items of many different types; but only a single prey (e.g. school) can be pursued and handled at a time.
- 2) The predator is at equal risk (e.g. predation) per unit time while at the patch, in transit or at the central place.
- 3) Prey types available in a patch are encountered randomly in accord with a Poisson process, so that the expected time to the next encounter with a prey of type i is not conditioned on the length of time the predator has been searching unsuccessfully in a patch. This assumption should be true if the foraging patch is large and the predator lacks precise knowledge of the number of prey in a patch when it starts foraging there.

The effect of the use of aerial spotters, limits on landings and other characteristics of the anchovy fishery upon these assumptions will be discussed later.

Single school captured

A graphic model for the situation when a fisherman captures only one school per trip (for most anchovy fishing boats there is only one set made per trip due to vessel capacity or landing limits) can be seen in Figure 59. This graph shows a solution to the case in which handling time per individual school is very short when compared to total travel time. This handling time is probably not very important for most purse seine and trawling fisheries (compared to the whole trip time), although for the anchovy fishery it may take significantly longer to pump a very large school on board. Handling time may be more important for sport fishing and related fisheries, where it takes a long time to pursue and subdue an individual fish.

In the graphic model in Figure 59, traveling time is plotted to the left of the origin

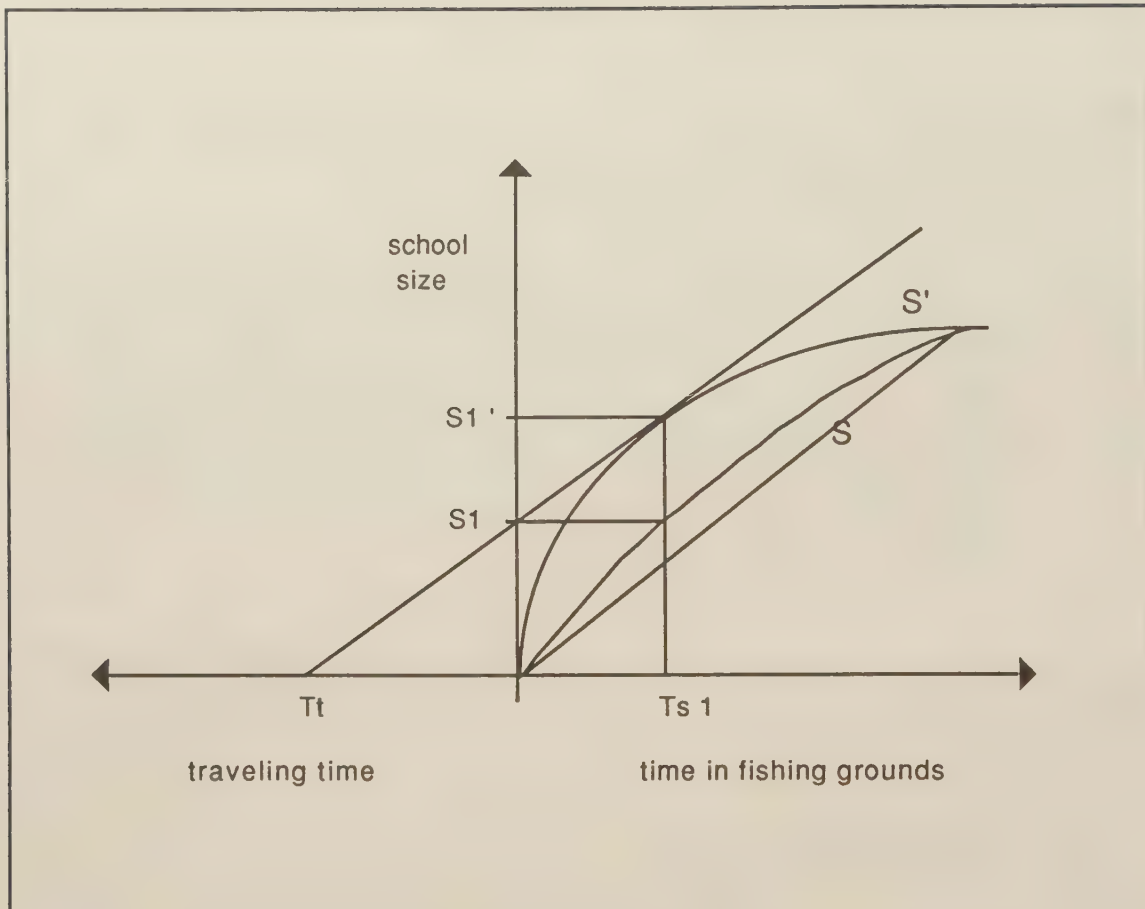


Figure 59. Central Place Foraging model for single school capture. Traveling time is plotted to the left of the origin and time in fishing grounds (handling, searching) to the right. The lower curve (S) represents school size versus expected time to find a school of size $\geq S$. The upper curve (S') represents the expected school size versus expected time to find a school size $\geq S$. Maximum delivery rate is then the straight line, tangent to S'. A fisherman should capture schools size $\geq S_1$ in order to maximize its expected delivery rate $S'_1 / (T_t + T_{s1})$. Adapted from the original model by Orians and Pearson (1979).

and time in the patch (fishing grounds) to the right. The lower curve (S) shows the size of a given school versus expected search time to encounter a school of size $\geq S$. As Orians and Pearson (1979) demonstrated, the exact form of this curve depends on density of schools in the locality under consideration; but regardless of school abundance, the curve should increase monotonically because a finite number of schools is being considered. The upper curve represents expected school size (S') versus expected search time to encounter a school of size $\geq S$. The average school size S' resulting from a strategy of capturing only schools with size $\geq S$ is bounded by S in the lower end and the maximum school size available in the region in the upper end. The two curves are related because a tangent through any point in the upper curve intersects the ordinate at the corresponding value of the lower curve for that same expected searching time point. This property makes S' increase at a decreasing rate (the formal demonstration is in the appendix in Orians and Pearson 1979).

It can be seen from the graph that a fisherman should capture any school size $\geq S_1$ in order to maximize its expected delivery rate $S'_1/(T_t+T_{s_1})$, that is, the average capture per unit time delivered over many trips (capture S' , divided by the sum of traveling (T_t) and searching (T_s), times). In this graphic model, the maximum delivery rate to the central place is then the tangent to the upper curve (straight line in Figure 59) which intercepts the abscissa axis at a given round trip time, and the minimum school size necessary to achieve that maximum rate is the intercept at the ordinate axis. The two most important conclusions arising from the model are:

- As distance, and hence traveling time from the central place (e.g. fishing port) to the fishing site increases, the lower the delivery rate should be. If the roundtrip time increases, the slope of the tangent should decrease. This should be true unless school density increases with distance from port.
- As distance to the fishing site increases and the delivery rate to the port decreases, the greater must be the size of the school selected in order to make this -decreased- delivery rate to the central place the maximum possible for that distance. It can be seen in the model that as roundtrip time increases (to the left of the origin), the tangent to the C' curve intercepts the ordinate axis at a higher point.

Figure 60 shows the delivery rate (in catch/hour/trip) of a single boat from the Ensenada fleet for the years 1978-1985 (except 1979 and 1981) versus the distance at which the set was made from the port. Vessels from the Mexican fleet are better for this study because there is less aerial scouting (e.g. complete information assumption) and no landing limits. The delivery rate index was calculated using this distance and an average travel time of 8.5 nm/hour to calculate total roundtrip time in hours. Handling time was considered negligible. Although the points are very scattered, there is a clear tendency of the delivery rate to increase (up to 45 tons per hour) at distances of less than 20 nm; and to decrease (to less than 20 tons per hour) at distances higher than 65 nm. Between 20 and 65 nm, however there is no apparent relation, indicating no effect of distance on delivery rate. Nevertheless, the overall tendency is for the delivery rate to decrease ($r = -0.45$) with increased distance from Ensenada.

Figure 61 shows data for the same boat and years. Catch per trip is plotted against distance from Ensenada. Catch per trip is considered an indicator of the average school size captured because this boat made only one set over a single anchovy school during most trips. Again, below 30 nm from port, the average captured school tends to be smaller. No school larger than 200 tons was captured within 40 nm from Ensenada; while at higher distances (more than 50 nm) the average catch per trip increases to approximately 200 tons. There is a clear tendency of catch per trip to increase with increased distance ($r = 0.36$). Scatter of points is, as expected, higher at large distances. It is also interesting to notice that the lower limb of the envelope of points levels at around 30 tons. This is probably the result of the constraint of fixed total fishing time (due to fuel and other vessel requirements). Under these conditions, near the end of an unsuccessful fishing trip, the best strategy may be to follow the principle of "last opportunity", that is, to capture any school encountered disregarding size. This situation will be examined in detail in the section on the anchovy fishery case.

Therefore, delivery rate could be arguable increased if a predator modified its prey selection policy during a foraging trip, so let's consider now what happens if a fisherman changes his strategy as a result of the time already in an area unsuccessfully looking for a certain minimum school size. A graphic solution to the problem is shown in Figure 62 (based on the original model by Orians and Pearson, 1979) in

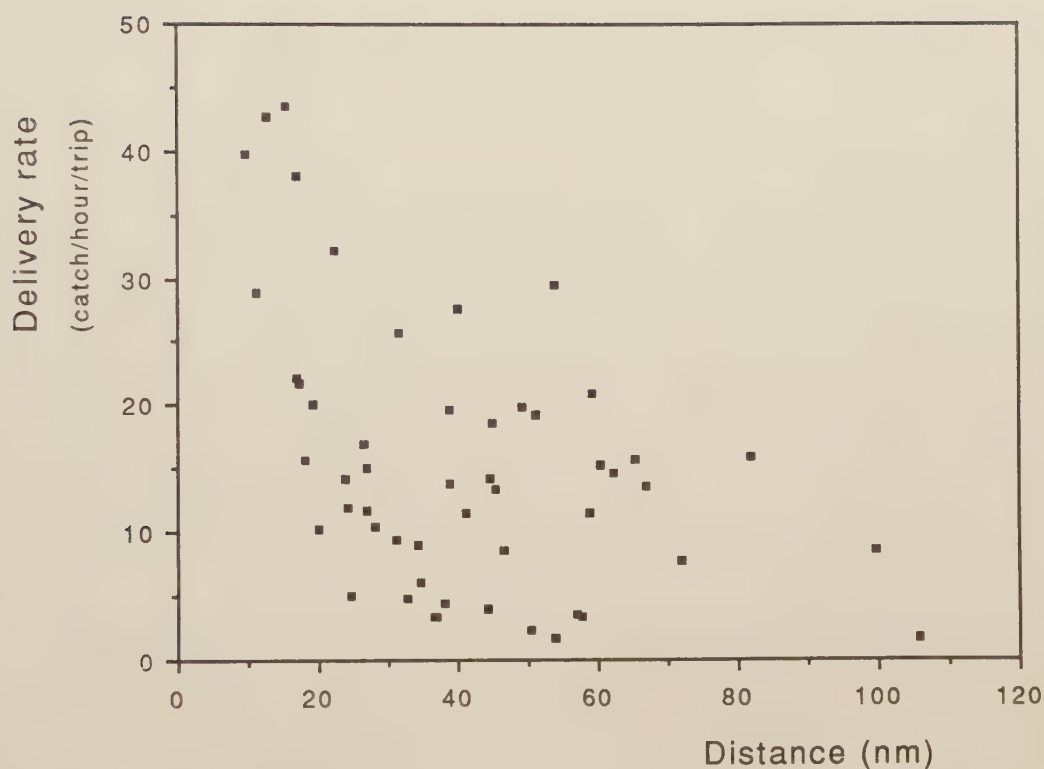


Figure 60. Delivery rate and distance from port. Delivery rate of a single boat from the Ensenada fleet (from 1978 to 1985) is shown. Although the points are very scattered, there is a clear tendency of the delivery rate to decrease with distance from port. The higher delivery rates were obtained when fishing took place at less than 20 nm from Ensenada.

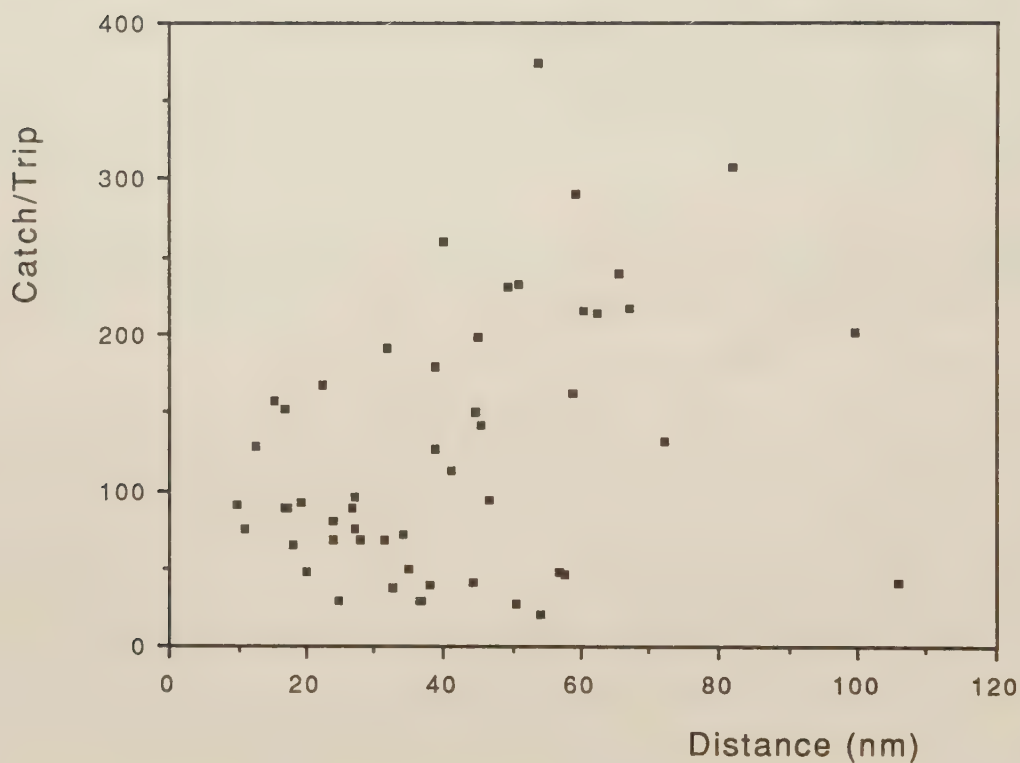


Figure 61. Catch per trip and distance from port. Average school size captured (catch per trip is used as an index of school size because the boat made only one set per trip for most trips) is plotted against distance from Ensenada for the same vessel and years as in Figure 60. As expected, below 30 nm from port the average captured school tends to be smaller; while at higher distances the average school size captured increases.

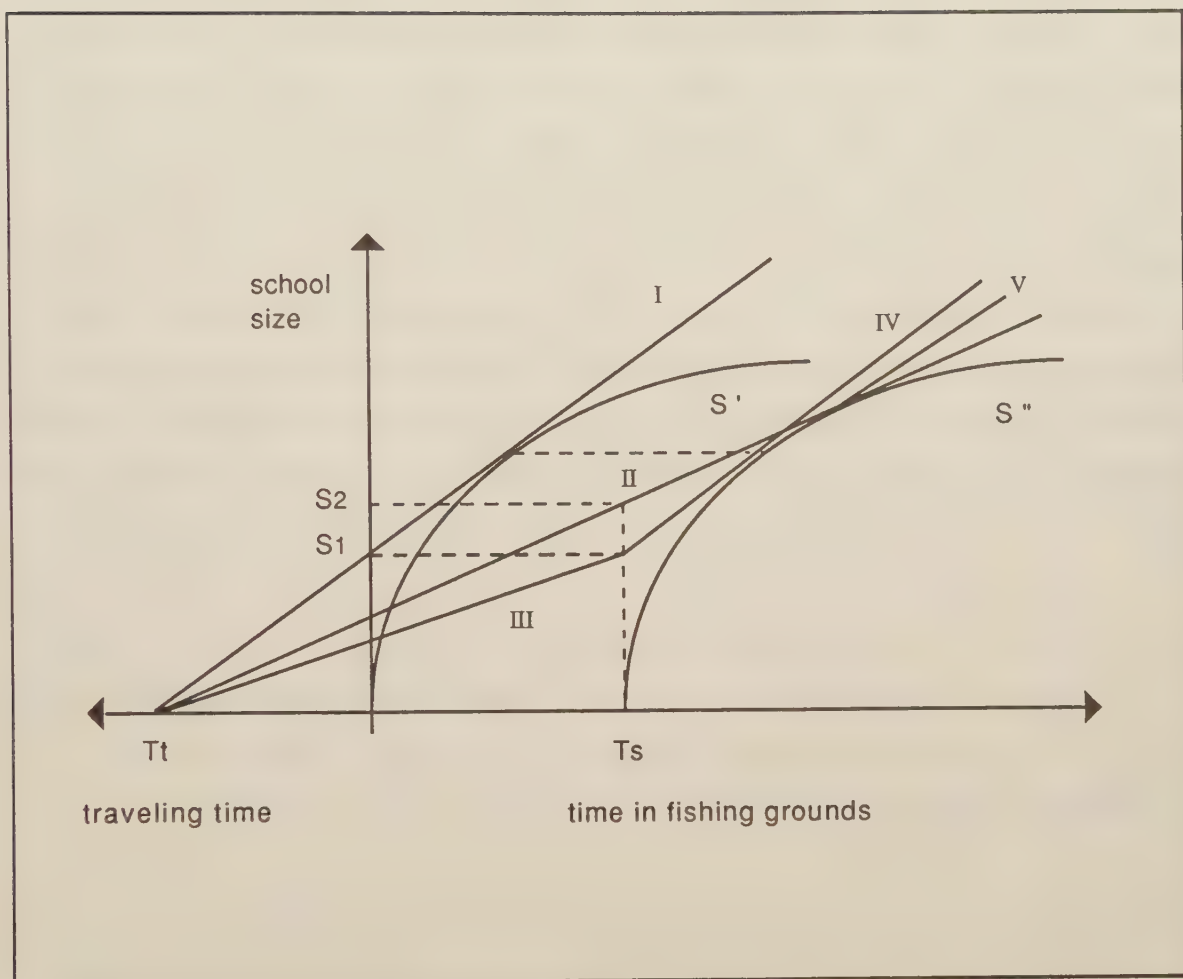


Figure 62. Change of school selection strategy as a function of unsuccessful search. Altering the search strategy can increase delivery rate for a particular trip, but reduces the long term expected delivery rate. T_s is now the actual time spent searching in an area when a school of size S_1 is encountered. The fisherman should decide now whether to capture S_1 or to change strategy. S'' curve is the S' curve displaced to the right by an amount T_s . Slope of lines I to V are the expected delivery rates under different strategies. See text for explanation. Adapted from Orians and Pearson (1979).

which a fisherman already in the fishing grounds has just encountered a school of size S_1 at an elapsed search time T_s (higher than expected for that school size at the onset of the trip), and must decide whether to harvest S_1 or change his policy to follow a strategy of capturing only schools of size $\geq S_2$.

The S' curve is the same previously described as the expected value of a school versus the expected search time to find a school $\geq S$. Curve S'' is the same as S' except that it has been shifted to the right due to the elapsed time (T_s) before finding a suitable school. As we saw before, the slope of line I represents the maximum delivery rate expected at the onset of the trip, and it is fulfilled by taking schools $\geq S_1$. The slope of line II gives a revised maximum for that trip, after taking into account (by moving the curve to the right) the elapsed time T_s for a successful search, and it is clearly lower than I, since no appropriate schools were found during T_s units of time. In order to achieve this revised maximum, however, the selection should now be limited to schools $\geq S_2$, where S_2 is always higher than S_1 . The slope of line III represents the actual delivery rate if school S_1 is taken when found at time T_s . This rate is clearly lower than that represented by line II, achieved capturing only schools $\geq S_2$.

However, a comparison of lines IV and V, where the slope of line IV is the expected cumulative total value of schools versus elapsed time and the slope of line V is the expected total value versus total elapsed time for the revised strategy shows that line IV represents the best strategy, that is, taking schools $\geq S_1$ whenever encountered is better on the long run.

A corollary of this analysis is that altering a fishing strategy as a response to unsuccessful fishing may increase the delivery rate for a particular trip; but reduces the rate averaged over future trips (slope of line IV is slightly higher than slope of line V). Orians and Pearson (1979) found that this apparently strange situation, in which maximization of size per unit time per trip does not necessarily result in maximization of the total size delivered per total time fishing can be explained by the fact that not only the value of the capture per unit time per trip should be maximized; but more trips should be taken in the available time to average out the effects of a particularly bad trip, and these two quantities can not be independently maximized. Also, the long term (e.g. over a fishing season) average rate maximization is probably more realistic to the fisherman because it is more important to evaluate the outcome of a series of fishing decisions than the result of a particular trip

(Stephens and Krebs, 1986).

When handling time is explicitly considered, some results are different. In this particular case, already developed OFT can be applied; the ranking of schools in descending order takes place not only according to its value and handling time, but also taking into account the roundtrip time necessary to capture it. Thus, the same school can be ranked in a different position if found at different distances from the fishing port. Under these conditions, the combination of school size and handling time should be more important to the fishermen when selecting a school near the fishing port. However, when travel time is large, the relative importance of handling time diminishes, and the importance of a school depends more on its absolute size. Therefore, the optimal fishing set should include mostly easy to capture (e.g. small) schools near the port and predominantly schools of larger size when distances increase. A mixture of both school types should be caught at intermediate distances, but as it was shown in the previous section, breadth of "diet" will depend only on the availability of high ranked schools in a particular area.

Multiple schools captured

It has been argued (Lessells and Stephens, 1983) that the solution to the single prey captured described above can be applied only to the multiple prey situation. The authors propose that the qualitative results are similar in both cases, but that the underlying assumptions of each situation are completely different.

The argument (adapted to a fishery situation) is simply that the S curve does not pass through the origin (see Figure 63) because when S is zero, there is an expected search time of zero, and a fisherman expects to return to port with a school of zero size (e.g. no school). This situation is clearly anomalous; therefore, the S curve should meet the abscissa to some point to the right of the origin. The authors also point out that the S' curve has no values below the minimum expected searching time and that both lines (curve S and curve S') converge when the value of the prey item is the maximum for that area. The most important result of Lessell and Stephens is that there is a critical time (at a distance near the central place) below which the forager should be unselective. The best strategy under these circumstances is to take

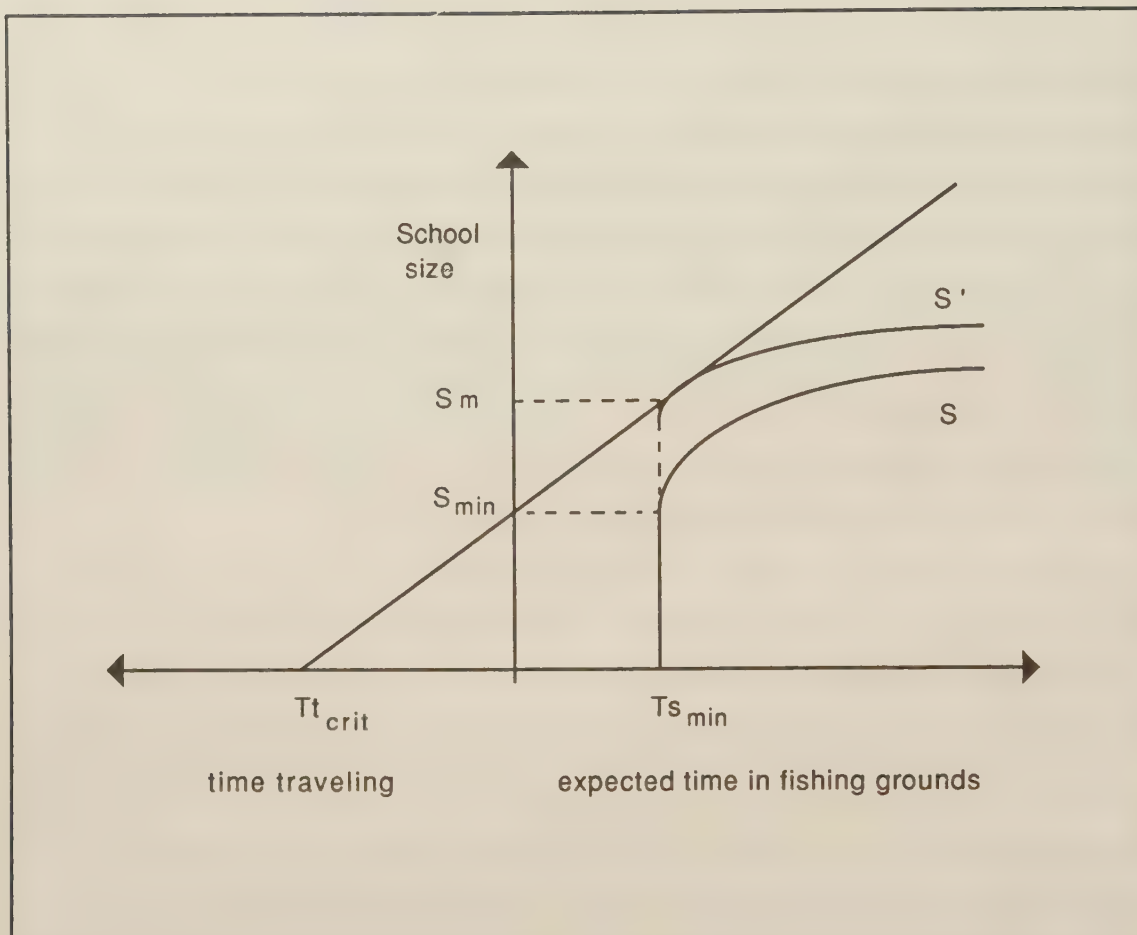


Figure 63. Basic CPF model critical travel time modification. Since the S curves do not pass through the origin (see text), fishermen should be unselective below a critical travel time ($T_{t \text{ crit}}$). At any travel time below the critical T_t , any tangent to the C' curve must meet the C' curve at the point where $C' = S_m$ (mean size of available schools in the area). S_{min} is the minimum school size available, with an expected searching time of $T_{s \text{ min}}$. Based in Lessells and Stephens (1983).

any school detected. The average school size captured in this case will reflect the mean school size available near the fishing port.

Despite these differences, the qualitative results are the same as in Orians and Pearson's model; furthermore, they are similar for both the single and the multiple school captured cases: expected delivery rate to the central place decreases with increased distance, and minimum school size required to achieve the expected delivery rate increases with distance. In summary, Lessells and Stephens (1983) consider that only for the single prey capture case the S curves will actually start at the origin, as Orians and Pearson (1979) originally proposed.

Therefore, in the multiple school capture case (i.e., a tuna boat that can capture many individual schools over the span of a 3 to 6 months fishing trip), if the overall quality of a given area remains constant, optimal load (e.g. number of schools taken) increases with increased distance from port. A vessel should continue to capture schools until full capacity even if its catch rate is decreasing. Catch rate could diminish due to a variety of causes, among them resource depletion effects and increased difficulty (time and energy needed) in the handling of each new individual school (Bryant and Turner, 1982). Also, if the quality of the area decreases but travel time remains constant, the optimal load should decrease slightly; however, the time spent in the fishing place should increase significantly since it takes more time to locate an adequate school (Orians and Pearson, 1979).

Overhead Cost

Figure 64 shows the effects of overhead cost (i.e. fuel and boat maintenance expenditures) in the multiple schools captured model. Cost can be considered to be a negative value in the ordinate axis, and its effect will be to lower both curves. Therefore, the overhead cost problem is equivalent to lowering the quality of a particular fishing site, thereby forcing fishermen to stay longer in order to find suitable schools. In the graphic model of Figure 64, the optimal time at the fishing area changes from T_{s_1} to T_{s_2} as the curve is lowered due to overhead costs. For a given distance (e.g. roundtrip time) the expected delivery rate should be lower when costs are considered; in Figure 64 it decreases from the slope of line I to the slope of line II; the optimal load also decreases, changing from S_1 to S_2 .

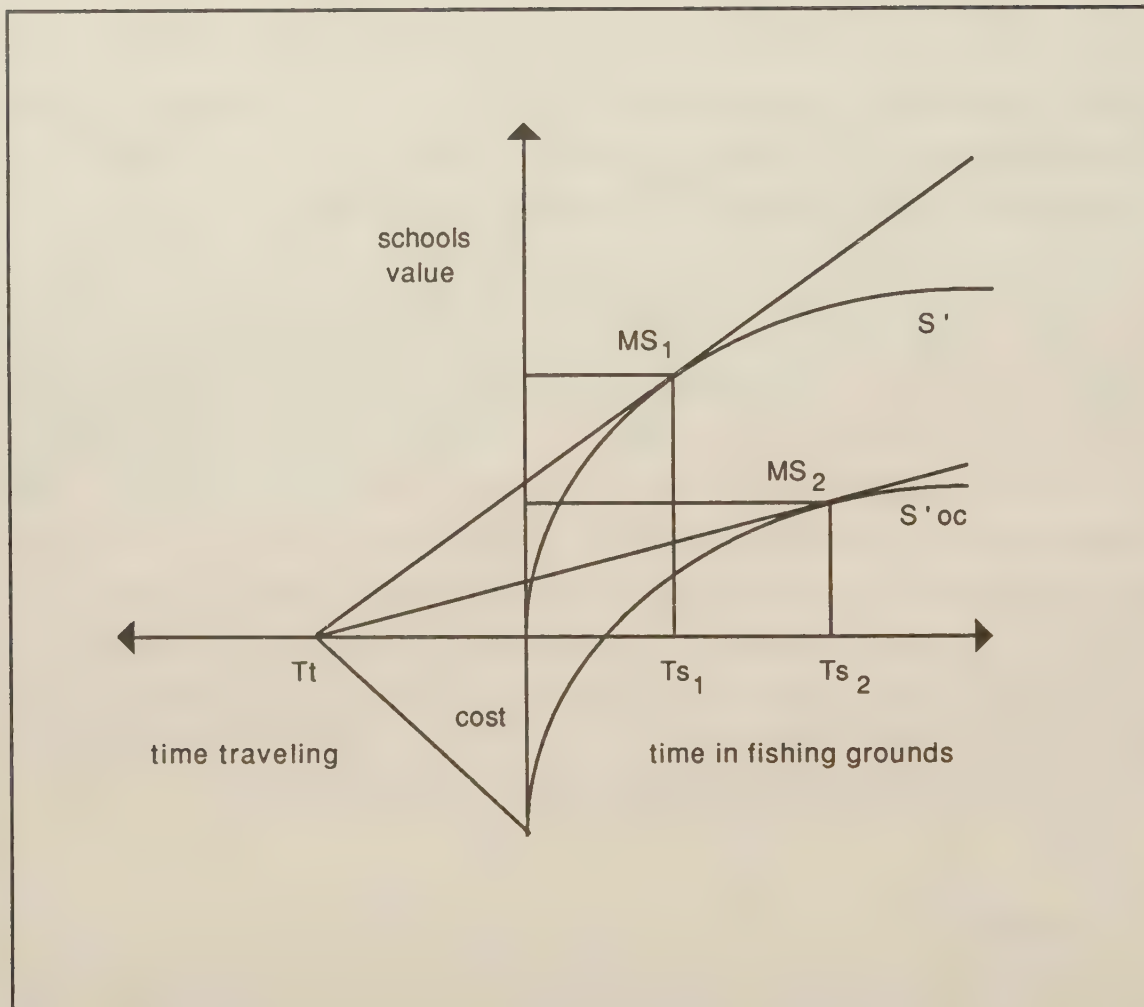


Figure 64. Effects of overhead costs. The optimal load for a multiple schools case is shown with (curve S'_{oc}) and without (S') consideration of overhead cost. Overhead drives the C' curve down and increases time in fishing grounds from Ts_1 to Ts_2 . The value of schools captured also decreases from MS_1 to MS_2 . Based on Orians and Pearson (1979).

The Anchovy Fishery Case

If we consider the particular case of the anchovy fishery under the basic model in Figure 59, some adjustments have to be made to fit the nature of the system under consideration. Basically, the fishery is operating under the following constraints and characteristics :

- 1) Since this is mostly a night fishery, there is a limited amount of time available for the total trip, which is usually between 12 and 24 hours. This maximum total time imposes limits on time searching in a particular fishing site and total time in the general exploitation area, as well as on traveling time. The optimal allocation of time (i.e. traveling versus searching) is probably an issue as well.
- 2) As we have seen in the previous chapter, the U.S. canneries impose a limit on landings. This limit varies with the price of fishmeal; but for several years it has been set at 40 tons. This implies that some boats may not always be allowed to harvest their total capacity, so there is a maximum size of school of interest to fisherman that probably limits also the time of staying in a particular area.
- 3) There is an inshore closure in the U.S fishery. This area closure is usually three miles (in some areas like Santa Monica Bay is up to five miles) from the coast, where no reduction fishery is permitted. This area closure imposes a minimum travel time necessary just to get to the legal fishing grounds. There is no equivalent closure for the Mexican fishery, except for the prohibition to fish within the Ensenada Bay area, which is less than 3 miles wide but forces fishermen to leave the bay before they start searching for schools.
- 4) As was described in Chapter II, the U.S. fishery uses the services of professional spotter pilots, which indicate to the fishermen the

approximate location and size of the schools in an area, sometimes helping with the setting of the net during the actual fishing operation.

Maximum total fishing time available

Due to fishery characteristics, such as the cannery need of obtaining a fresh catch, the lack of refrigeration systems in most boats and their limited fuel capacity load, there is a maximum total time available for fishing. The effect of this constraint, the limited duration of a fishing trip, is illustrated in Figure 65. The main factor to consider is that given a limited total time available for a fishing trip (T_{tot}), a fisherman must find the best time allocation for two conflicting activities that cannot be independently maximized: traveling to and from the fishing grounds and searching in the exploitation area for an adequate school size (as before, handling time is considered negligible). The critical distance or travel time in this model is $T_{t,crit}$, where the time left for searching after traveling ($T_{s,crit} = T_{tot} - T_{t,crit}$) is equal to the expected time needed (e.g. $T_{s,crit} = T_s$) to maximize delivery rate (slope of line I) for that particular trip.

At traveling distances smaller than $T_{t,crit}$, there is always enough time left for searching (because given a fixed T_{tot} , $T_t < T_{t,crit} \Rightarrow T_s > T_{s,crit}$), so that delivery rate can be maximized e.g. slope of line II can theoretically be achieved. On the other hand, when travel distance is greater than $T_{t,crit}$, the time left for searching is not large enough to find the school size necessary to achieve the highest delivery rate (slope of line III) for that distance (because given a fixed T_{tot} , $T_t > T_{t,crit} \Rightarrow T_s < T_{s,crit}$). This second alternative implies that delivery rate will always be suboptimal for all travel distances greater than the critical distance (e.g. for all $T_t > T_{t,crit}$) the slope of the delivery rate line will be smaller than the tangent to the S' curve for that distance. In the example, delivery rate will be smaller than the slope of line III. Furthermore, under the unlimited travel time assumption, the expected school size captured increases with distance (see Figure 61). However, with a limited T_{tot} the maximum school size to look for will be determined by available T_s left, so that maximum delivery rate can be achieved only at distances of less than the critical distance.

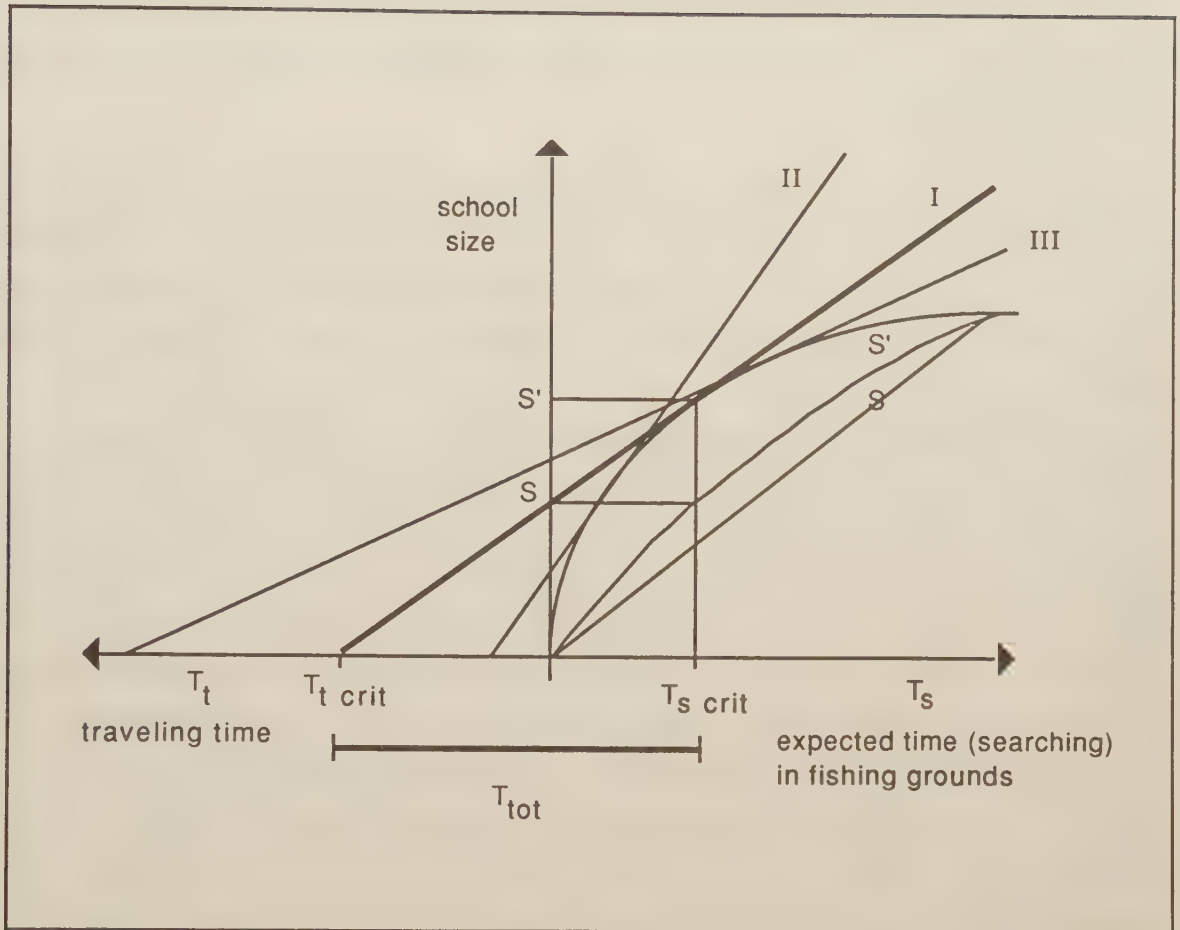


Figure 65. Effect of limited total time for fishing. The critical distance or travel time is $T_t \text{ crit}$, when time available for searching ($T_s \text{ crit}$) is equal to the expected time (T_s) needed to maximize delivery rate for that trip (slope of I). Below this critical distance, there is enough searching time left to achieve the maximum delivery rate (slope of II). However, for travel times above the critical time, the maximum delivery rate can not be achieved, because there is not enough time for searching. Therefore, delivery rate will be less than the slope of III.

Under these conditions, and taking into account that the expected delivery rate to the home port decreases with distance (see Figure 60) the best strategy is to stay as close as possible to the fishing port, allocating as much time as possible for the searching of large schools. This limited total time constraint implies therefore that for a given situation (e.g. a given T_{tot}) there is a maximum distance and school size a fisherman should look for in order to maximize delivery rate. This constrained fishing strategy will produce the concentration rings in fishing effort and landings described in Chapter II.

Figure 66 summarizes the effects of the total limited fishing time constraint. The limit on total time available (T_{tot}) imposes a maximum roundtrip time for traveling ($T_{t,max}$), which in turn imposes a maximum possible search time ($T_{s,max}$) that conditions the maximum school size to look for (S_{max}), producing a maximum expected school size (S'_{max}).

Thus, this constraint sets the upper limits of the system. Fishermen can not travel more than distance ($T_{t,max}$) or look for a school greater than S_{max} if they want to optimize the delivery rate to the fishing port. The slope of the straight line is then the minimum optimal delivery rate for the system, obtained at the maximum possible distance at which such an optimal rate can be achieved. Also, the limitation in time available for searching will produce a suboptimal delivery rate for harvest at any distance with roundtrip time beyond the critical time $T_{t,crit}$ (see Figure 65). The combination of this phenomenon and the increased likelihood that the principle of "last opportunity" (e.g. if fishing has been unsuccessful, take any school available when near the end of the total fishing time) be operating in this situation, may account for the observed low catches at distant places from Ensenada (see Figure 61). This result is consistent with that by Houston and McNamara (1985) which found that the minimum acceptable food item is a function of total time spent foraging.

Limit on landings

The situation depicted in Figure 67 is the second constraint, the limitation on landings imposed by the canneries. If the limit is set at a school size of S_2 , fishermen should follow a policy of taking only schools $\geq S_1$, in order to obtain an expected size of S_2 ($S_2 > S_1$), with a maximum travel time of $T_{t,max}$ and an optimal delivery rate. The

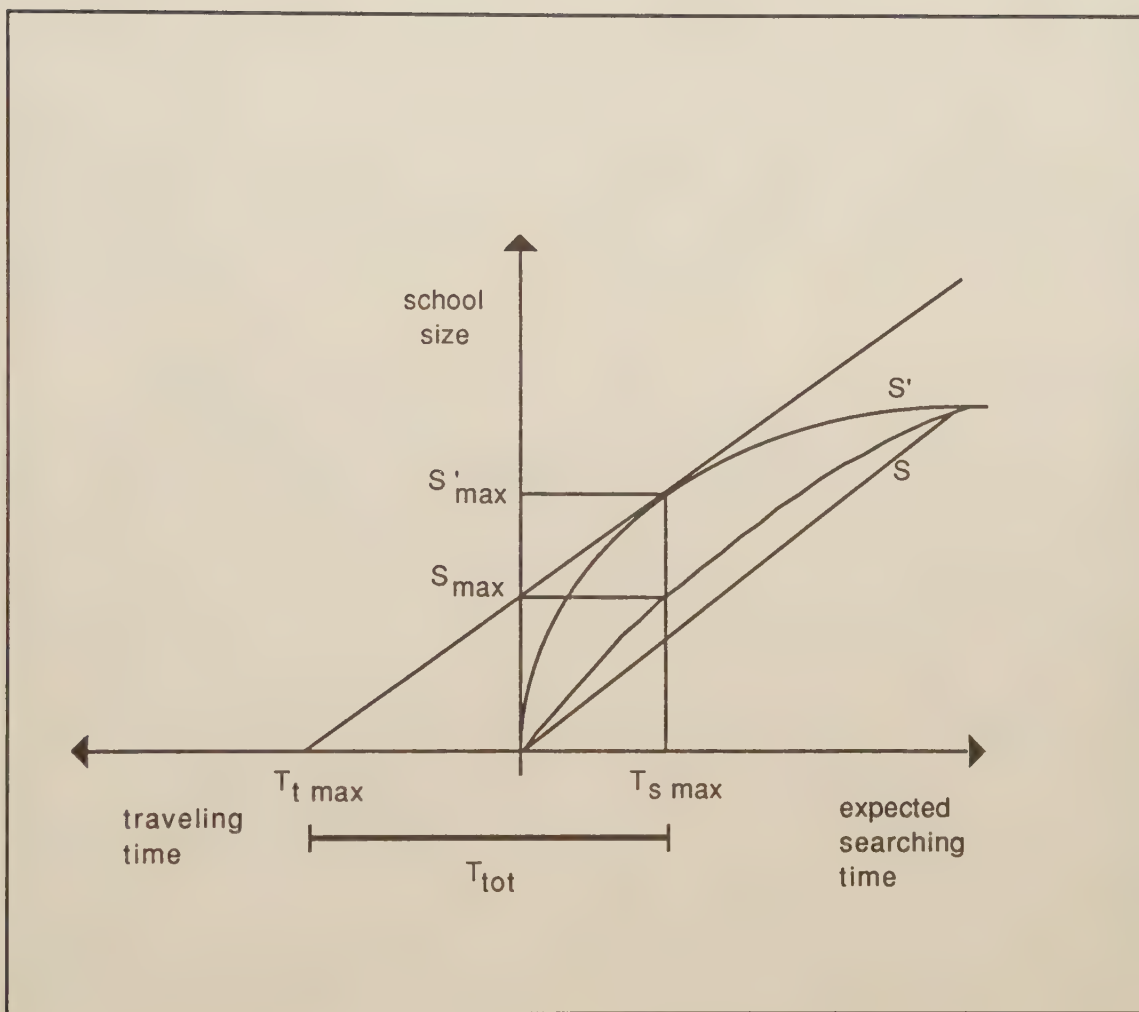


Figure 66. Upper limits of the system under the limited time constraint. Fisherman cannot travel more than distance $T_t \text{ max}$ or look for a school larger than S_max (with a expected $T_s \text{ max}$) in order to optimize delivery rate to the fishing port. The slope of the straight line represents then the minimum "optimum" delivery rate for the system, achieved at the maximum possible distance for a given total fishing time (T_tot). See Figure 65 and text for explanation.

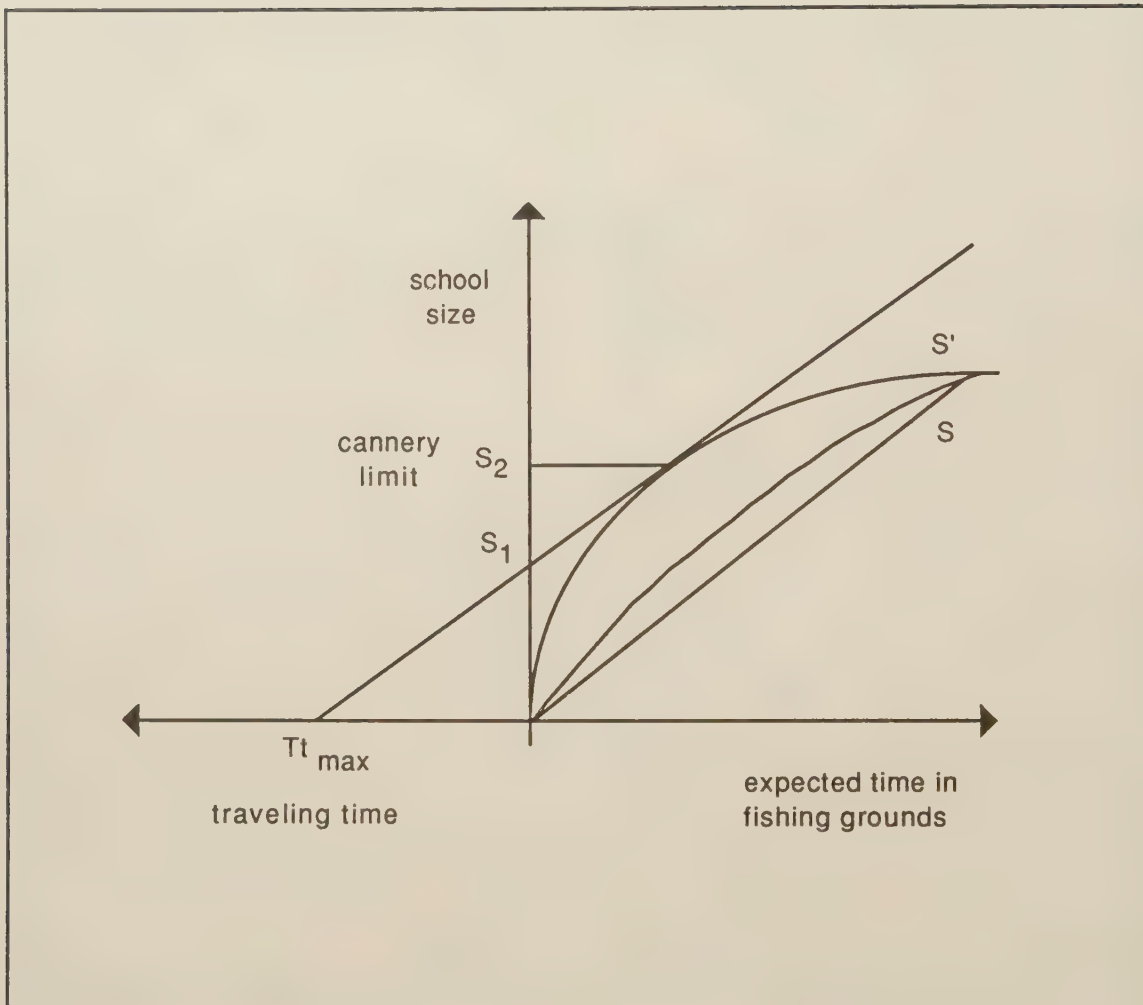


Figure 67. Effect of cannery limits. If the canneries set a limit of S_2 in landings, fishermen should look for schools greater or equal to S_1 in order to achieve an expected school size of S_2 ($S_2 > S_1$). The maximum travel time is then Tt_{max} . The landing limit reduces the school size of interest to only two classes: $S = S_2$ and $S \neq S_2$ (either too large or too small) and reduces the effective area of the fishery.

number of school types in the optimal set is in effect reduced to only two, depending on whether they are equal to S_1 or different, either too large or too small.

Therefore, any upper limit imposed in the catch, will have the effect of reducing the maximum distance fishermen are willing to travel, decreasing the effective area of the fishery, and making the boats operate as close to the port as possible. This effect will be strong if the selected limit is at the middle portion of the range of school sizes available, and weak if the limit falls in the upper or lower portions of the available school size range (that is, when the difference between what the fishermen are looking for and what they get on the average is small). If the cannery limit approaches the maximum school size found in the area, the effect is negligible. If it approaches the lower sizes, then the best strategy is to take any school size whenever encountered.

In summary, a cannery limit makes the fishermen look only for a certain school size. Above this imposed size, the schools are of no interest unless the boats take only part of the school during the set (however, this graphic model assumes that complete schools are taken and delivered to the fishing port), which sometimes can be quite complicated (e.g. at certain periods of the year large schools are dangerous to catch as they may cause the boat to sink due to the negative buoyancy tendency of the fish). Below this school size they are also of no interest (if there is only one set per trip). This implies that there are only two school categories: those 'good' due to the cannery limit, and those (either too large or too small) of no interest. Additionally, the maximum distance fishermen are willing to travel is also limited by the cannery limit. Thus, under this cannery limit constraint (of major importance for the Southern California fleet) fishermen are looking actively for a limited school size range in a restricted area.

Area closure

A solution for the area closure constraint effect is shown in Figure 68. In this graphic model, the area closure decreases delivery rate, excluding higher slopes by imposing a minimum distance traveled from T_{u1} to T_{u3} . Under these circumstances, the maximum delivery rate is achieved by fishing just a little beyond the inshore closure. The school size sought to obtain the highest delivery rate increases from S_1

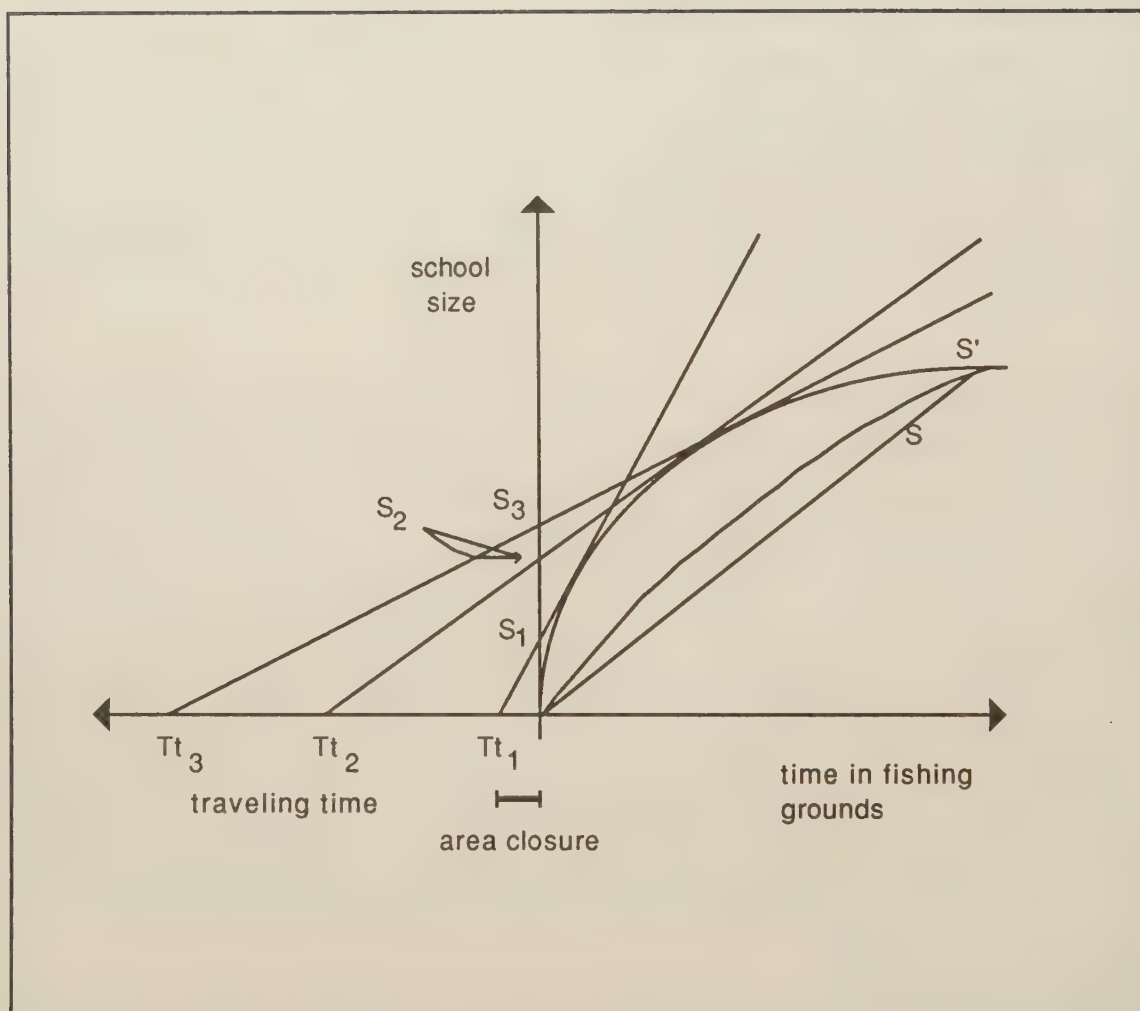


Figure 68. Effect of area closure. Small increments in the minimum distance fishermen must travel due to the area closure in the inshore region will lead to large increments in the minimum school size fishermen need to look for in order to maximize delivery rates. A change in area closure from Tt_1 to Tt_3 will change the school size sought from S_1 to S_3 . However, a change in an already large area closure (e.g. from Tt_2 to Tt_3) will bring about a relatively small change in school size (from S_2 to S_3).

to S_3 as does the expected search time.

As it was shown in the basic model of Figure 59, the expected delivery rate decreases with distance traveled, and the minimum school size fisherman should look for in order to maximize their expected delivery rate increases with distance from port, but at a decreasing rate. Therefore, if the area closure forces fisherman to travel to very distant places (e.g. from T_{i1} to T_{i3}), the minimum school size needed to maximize delivery rate to port remains almost the same (school sizes S_2 and S_3 are approximately equal). The effect is, however, very large for the inshore area closures where a small change in the minimum distance traveled may force fisherman to look for schools significantly larger than before. Also, the expected optimal delivery rate will decrease very rapidly with short increments in area closure in the inshore region.

Thus, the area closure constraint is very important in the inshore area, both in terms of changes in the average school size captured and in terms of decreased delivery rate to the fishing port. The effect of increments in an already large area closure are relatively small. This model and the graphic solution can therefore be used to estimate the economic effect or cost of area closures in terms of the school sizes fishermen are forced to ignore in order to obtain an optimal delivery rate under a given area limitation.

Use of scouting airplanes

The main consideration under this constraint is that the use of airplanes may give the individual fisherman a precise, in advance knowledge of the number and location of schools in a particular area, so that the encounter rates may not follow a random process. Also, this complete information may be used by fishermen to change fishing strategy within a particular area as a function of unsuccessful fishing trip (see Figure 62). These conditions violate the basic assumption of Poisson encounter rates in the Central Place Foraging single school model.

On the other hand, the use of airplanes can be viewed as the increased searching capability of a single vessel. According to this point of view, the use of airplanes do not violate the assumption of Poisson encounter rates, but it just provides the

fisherman with an improved set of school detecting abilities. Information will still be incomplete, as the particular fishing vessel will not have position and size of all schools in an area.

Therefore, the aerial spotters increase the effective area searched thereby reducing time searching while increasing the expected delivery rate. Since the relationship between the S and S' curves is determined only by the relative frequencies of different school types and not by their overall abundance (Lessells and Stephens, 1983), the use of airplanes should not change the general shape of the curves. However, the use of aerial scouters will reduce expected searching time (overall time in fishing grounds will also be decreased accordingly).

One solution to the last constraint in the anchovy fishery system, the problem of the use of spotter planes in the U.S. fishery, is shown in Figure 69. The solution in the graphic model is to move both the S and S' curves to the left by the amount searching time (T_s) is being reduced. This new arrangement modifies the position of the expected school size captured curve from S' to Sp' . As a consequence, the expected delivery rate for all distances will be higher. In the graph, for the same distance traveled (T_t) the airplane use should decrease expected search time, and should increase the delivery rate from the slope of line I to the slope of line II. However, this model predicts that both the mean school size caught and the school size sought should be smaller using scouting airplanes ($S_1 > Sp_1$; $S'_1 > Sp'_1$). This makes sense because the total time spent fishing is less, and therefore there is no need to look for large schools in order to maximize delivery rates. Also, notice that for a given school size of interest, the use of airplanes reduces the travel time and increases the delivery rate; that is, since searching is less time consuming due to improved detection capabilities, there is no need to travel that far or to look for large schools in order to maximize delivery rate to the fishing port.

Combined effects of constraints

The combined effects of the maximum travel time available for fishing, the limit imposed by canneries on landings and the area closed to reduction fishing in the U.S. fishery are illustrated in Figure 70.

The limited time available for fishing activities (see Figures 65 and 66) sets the maximum limits of the system by fixing the maximum travel time ($T_{t_{max}}$) and the

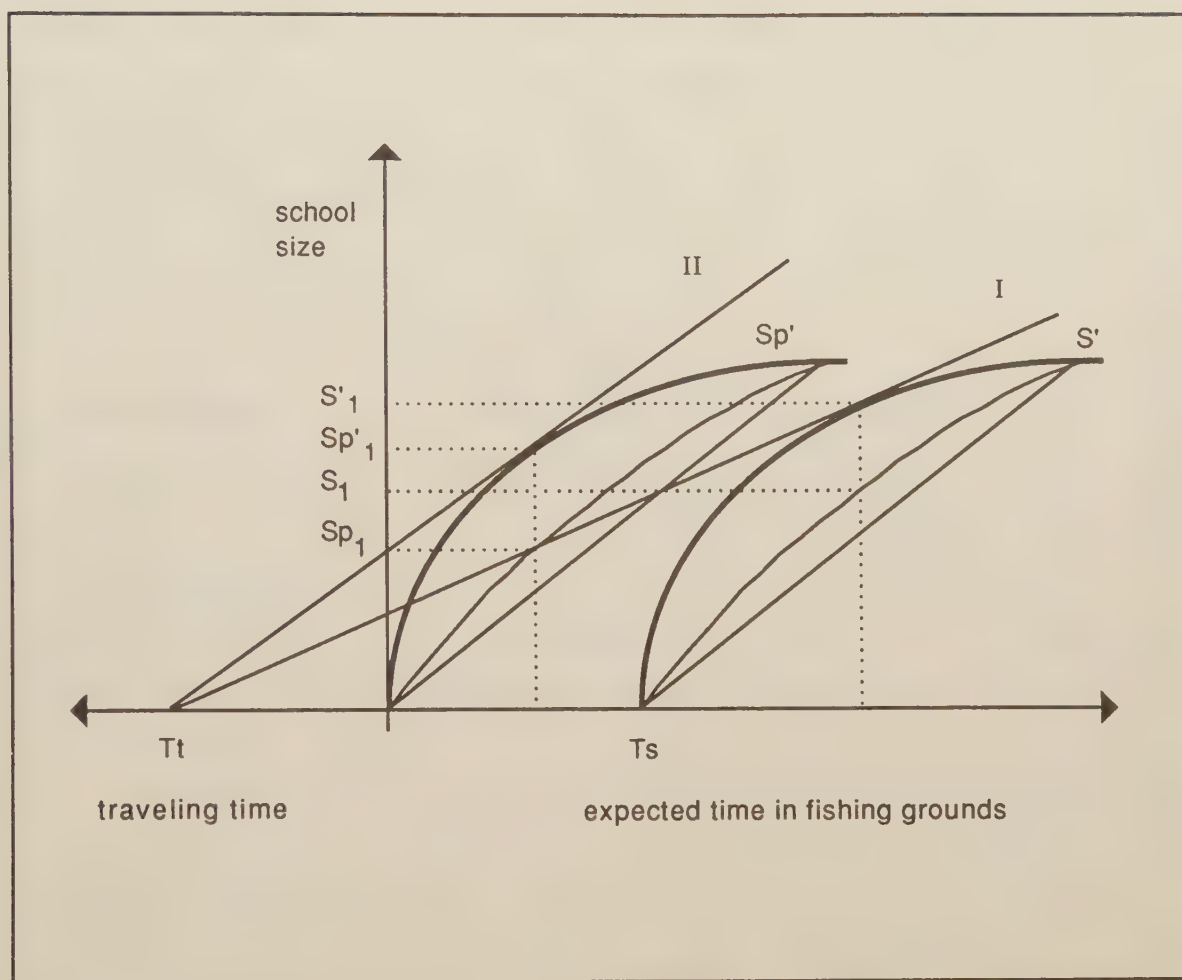


Figure 69. Effect of the use of spotter airplanes. The use of scouting pilots in the anchovy fishery should increase delivery rate in a particular trip (from slope of line I to the slope of line II), while reducing the mean size school captured ($S'_1 > Sp'_1$) and sought ($S_1 > Sp_1$). The $Sp - Sp'$ curves are the $S - S'$ curves of the basic model in Figure 59 displaced to the left by the amount of searching time reduced. The relationship between the curves remains the same because it depends only on the relative frequency of school sizes.

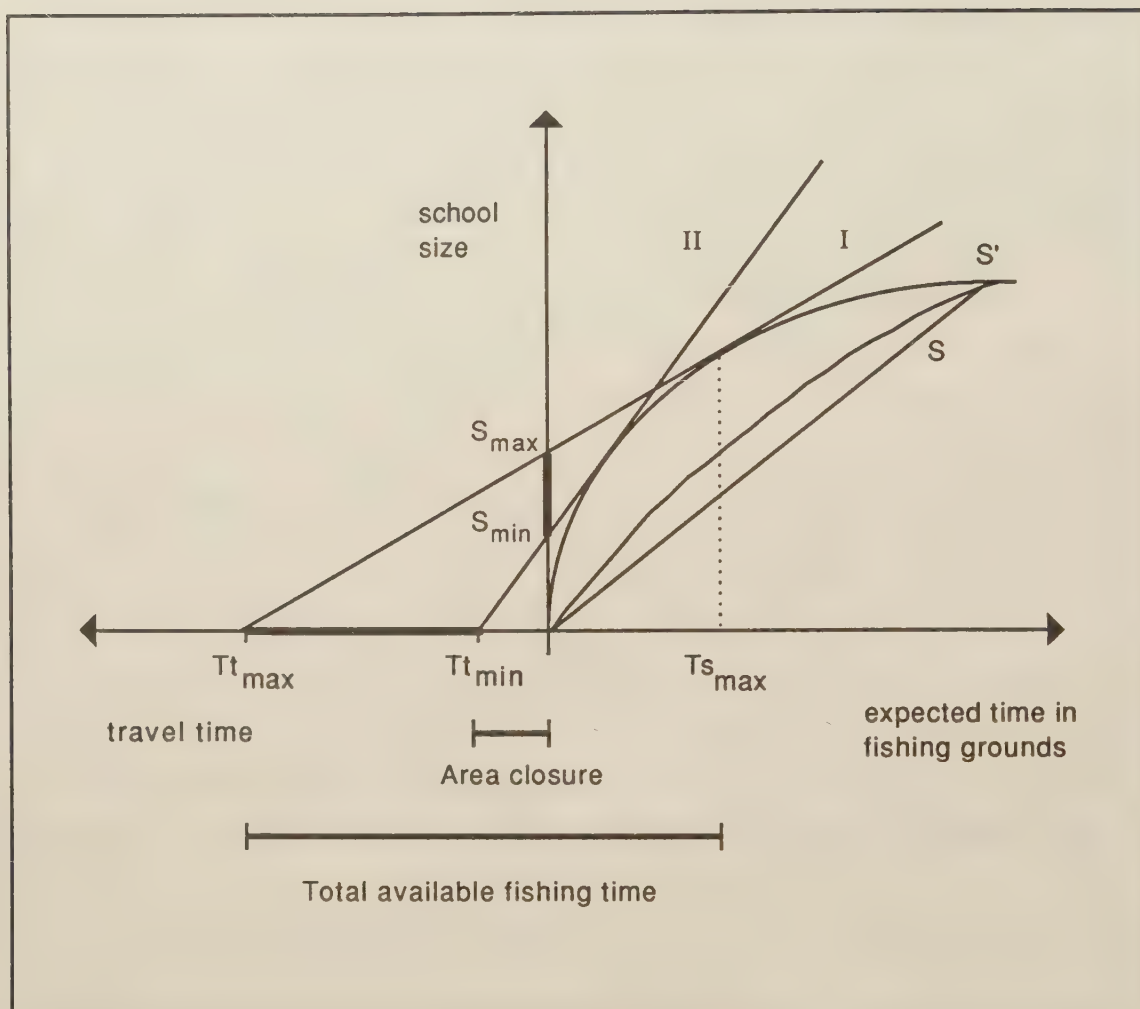


Figure 70. Combined effect of maximum fishing time, area closure and landing limits. The limited time for fishing sets the upper limits of the system: Tt_{max} , maximum travel time; Ts_{max} , maximum searching time; S_{max} , maximum school size sought and the minimum optimal delivery rate, the slope of line I. The area closure sets the lower limits of the system: Tt_{min} , the minimum mandatory travel time; S_{min} , minimum school size sought and the maximum possible delivery rate, the slope of line II. The landing limit operates between these two extremes. Its effect is trivial if the school sought is above S_{max} , but it will make the fishery to perform at suboptimal delivery rates if set below S_{min} . Together, these constraints define the spatial domain and the school size range of the fishery (thick lines).

maximum searching time left ($T_{s_{max}}$). These, in turn determine the maximum school size sought (S_{max}) and consequently produce the minimum optimal delivery rate feasible under the fixed fishing time constraint (slope of line I in Figure 70). Thus, the effects of this limited time are consequence of a tradeoff conflict between the time associated with travel and the time devoted to searching in the fishing grounds.

On the other hand, the nearshore area closed to reduction fishing works at the other end of the effect spectrum, setting a mandatory minimum travel time ($T_{t_{min}}$) by making fishermen to travel a fixed distance before they start fishing. Therefore, it excludes the higher delivery rates obtained by fishing as close as possible to the port (see Figure 68). The constraint also sets a lower limit on the school size needed (S_{min}) to achieve the slope of line II in Figure 70, which is the highest possible delivery rate obtained under the closed area restriction.

The limit on landings imposed by the canneries -which is usually related to plant processing capacity or to economic factors- operates between these two limits set by total time available and closure areas (see Figure 67). If the limit on landings is such that fishermen search for schools greater than S_{max} , it will be of minor importance for the spatial behavior of the fleet. Fishing activities should take place in the area delimited by travel times $T_{t_{min}}$ and $T_{t_{max}}$ and the best strategy is simply to catch any school that makes the delivery rate the highest for the distance traveled (any slope between the slopes of line I and II).

However, if the limit on landings is such that fishermen must search for schools smaller than S_{min} , then it will not be possible to obtain the highest delivery rate at any distance because fishermen must travel at least to $T_{t_{min}}$ before they can catch any school. Under this limitation, the best strategy is to fish just outside the closed area and look for a school as close as possible to the landing limit. In this way, delivery rate will not be optimal but the loss will be as small as possible, that is, delivery rate will approach the slope of line II.

The end result of these restricting factors is to make the anchovy fishery spatially constrained, exploiting predominantly the reduced area between $T_{t_{min}}$ and $T_{t_{max}}$. The other important effect is to reduce the number of school category sizes of interest to the fishermen, restricting fisheries attention to school sizes between S_{min} and S_{max} .

Even more important, due to the balance and interaction between the different

constraints, the anchovy fishery is extremely sensitive to both economic factors (e.g. changes in fish meal price) and biological variation (e.g. changes in spawning biomass). For example, a low limit on landings may drastically affect the fishery, because even fishing just outside the area closed and catching the largest possible school will not produce a delivery rate of sufficient importance to economically justify the fishing trip. Likewise, an increase in fuel price can affect $Tt_{\max}$ in such a way that the spatial range of the fishery will be severely constrained, and will not be possible to search for schools large enough to make the fishing trip economically worthwhile. As another example, both the S and S' curves will change size with changes in fish abundance, so that a spatially fixed area closed may have negligible effects one fishing season but it can make the fishery not economically viable the next year by excluding the higher delivery rates when fish abundance changes.

These results suggest that the graphic model on central place fishing can be used for management purposes. For example, it has been shown that setting the landing limit in such a way that fishermen must search for schools smaller than $S_{\min}$ will stop fishing because the limit does not allow high, economically good, delivery rates. This may be used as a regulatory mechanism because it works decreasing relative economic benefit.

The area closure (which is used to protect young individuals from fishing in the nearshore region) has the potential to be a powerful administrative measure as well. The restricted fishing area implies large traveling distances and consequently higher costs for fishermen. This in turn, implies the need to search for large schools to achieve economically satisfactory fishing delivery rates. Thus, changing the area closure size may achieve a dual purpose : on one hand, to protect the nearshore nursery areas and on the other to regulate the effort in the fishery by increasing the relative costs. This measure could be easier to accept by fishermen, because outside the closed area fishing would be unregulated. To be more effective, area closure measures could be coupled with information on biomass change and relative frequencies of the different school sizes available. In this way, the relative abundance of large schools should be enough to determine whether a fishing trip is or not economically advisable.

OPTIMAL PATCH MODEL

The problem of selecting a place in which to fish is formally similar to the problem of selecting a school type, although the nature of the problem and the important questions are very different (Stephens and Krebs, 1986). Fishing regions can also be added or dropped from the optimal set of areas according to their relative quality. The situation and selection issues are also analogous to the density dependent habitat selection problem (ideal free distribution) examined in Chapter I.

Fishermen should add and subtract more distant sites depending on the relative levels of school availability (e.g. relative levels of site quality). For example, in Figure 71 the time needed to obtain a fixed amount of harvest 'h' at a given place (a measure of the absolute quality of a fishing site) is plotted against the traveling distance to that area. In such a plot, sites of equal productivity -those whose combination of intrinsic quality and distance yield the same delivery rate to the fishing port- can be seen as lying along the same diagonal line with slope of minus one. In the graph, areas X and Y are equally rich in terms of school availability and relative abundance. They are equal because it takes fishermen the same time to obtain the desired capture. However, site Y will be preferred by fishermen because it is closer to the central port and consequentially it will yield a higher delivery rate than region X. However, as a consequence of school depletion due to harvesting activities, Y will eventually move to Y', where it takes longer to get the same amount of fish. At this point, (operating in an analogous form to the density dependent habitat selection phenomenon reviewed before) fishermen should switch places and start fishing in both Y' and Z because both places yield the same delivery rate (Z is closer to port, but its absolute quality is lower than that of Y').

The two major implications of this simple model are that delivery rate should be approximately the same for every place harvested when switching takes place; and that distant places are not harvested unless their absolute quality increases sufficiently to compensate for the higher traveling times.

The selection of a fishing site is analogous to the selection of a school discussed before in relation with the optimal prey model: in Figure 72 -also based in Orians and Pearson's (1979) work- each place has an absolute quality (e.g school abundance and availability) which determines the scale of the curve, and a distance from port which determines the displacement of the curve to the right of the origin. The

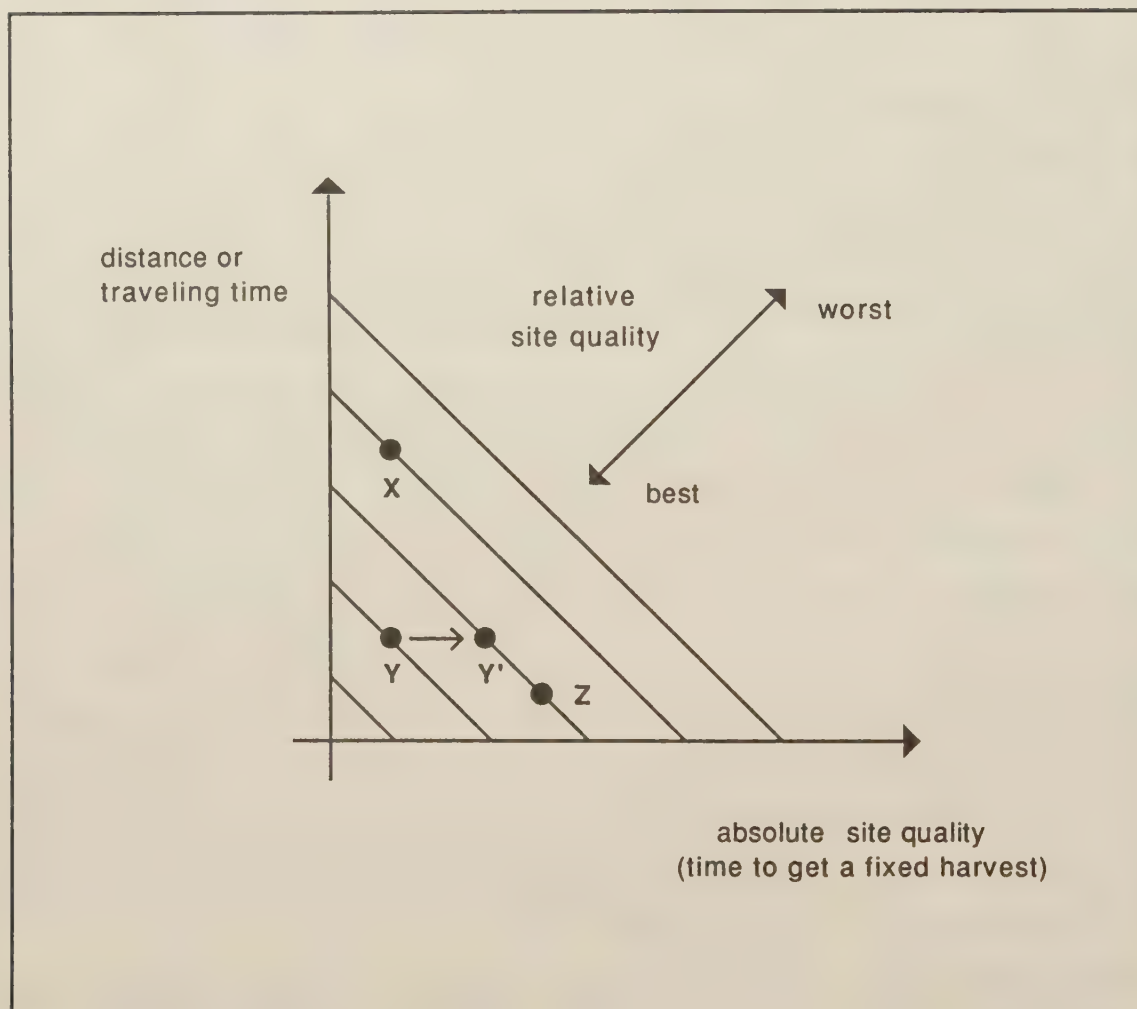


Figure 71. Fishing area quality and distance. Lines with slope of minus one connect places of equal productivity due to their combination of absolute quality and distance. Quality decreases in the abscissa axis. Places X and Y have the same absolute quality (e.g. same school density). The relative value of Y is however higher, because it is closer to port. When the absolute value of Y drops to Y' due to harvesting activities, both Y' and Z should be harvested, because Z is of lower quality but it is closer to the port. Adapted from Orians and Pearson (1979).

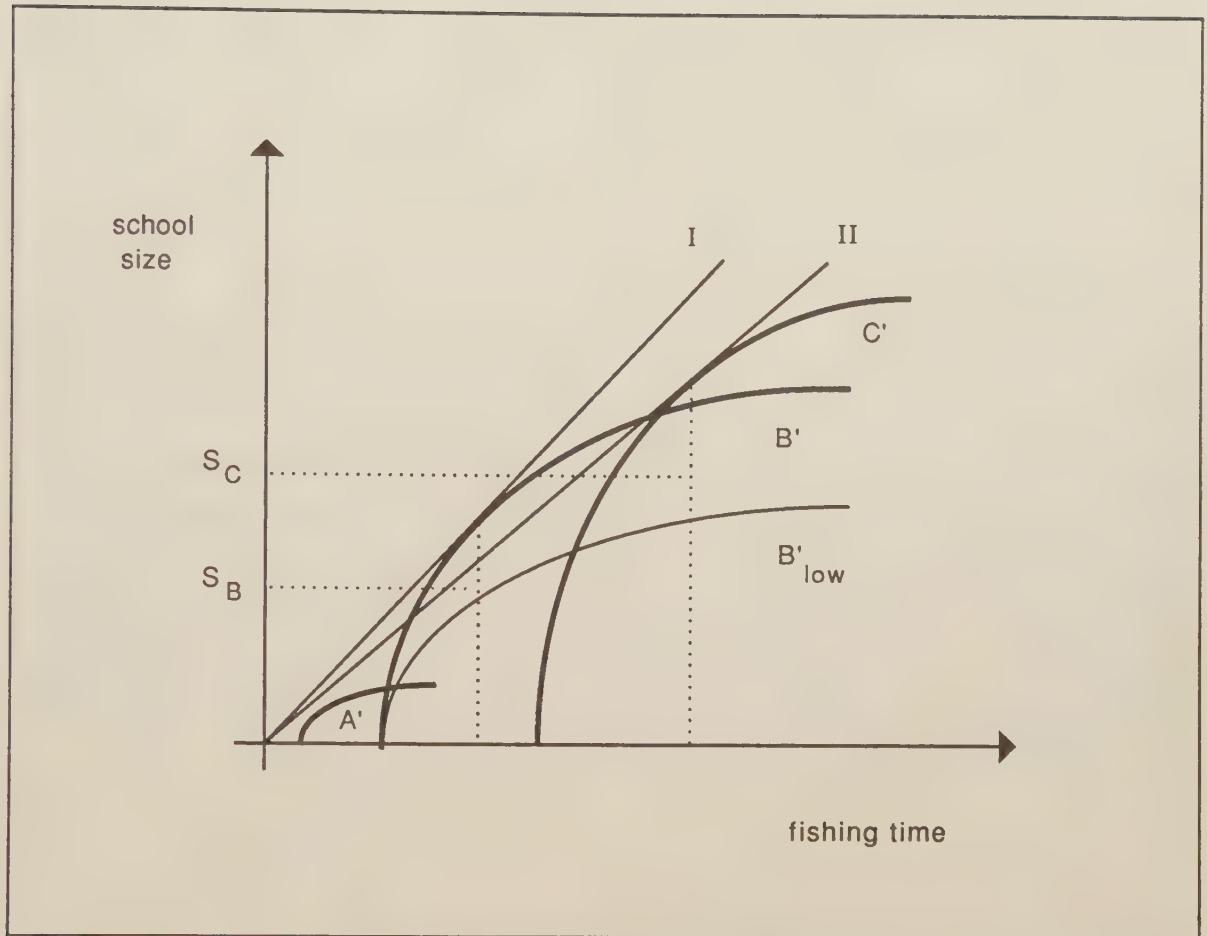


Figure 72. Relative value of fishing areas. A, B and C are areas of varying productivity situated at different distances from the fishing port. A', B' and C' curves are plots of expected searching time versus expected school size caught. The best fishing area is B, with delivery rate equal to the slope of line I and school size sought equal to S_B . If the quality of place B drops to B'_{low} due to fishing activities, then place C becomes the best fishing area, with delivery rate equal to the slope of line II and school size sought S_C . If a fisherman finds a school larger than S_B when traveling to B, it should be taken, as its delivery rate will be higher than the slope of line I. Place A should not be harvested despite being closer, because it is of lower quality. Adapted from Orians and Pearson (1979).

optimal solution is found as before by constructing a tangent to these curves, with the higher slope indicating both the maximum delivery rate and the place in which harvest should take place.

In the figure, A' , B' and C' curves are plots of the expected searching time versus expected school size caught for various fishing places at different distances from the home port (these curves are similar to the S - S' plots of the basic model in Figure 59). The curves are displaced to the right by an amount of time equal to the roundtrip time it takes to get to them. Area C is the richest, but also the most distant, so that the best combination of absolute quality and cost (in terms of distance traveled) is the area B. The slope of the tangent (line I) is the maximum delivery rate, obtained by searching for schools of size $\geq S_b$ in area B. Now, if when traveling to B a boat finds a school $\geq S_b$ it should be taken, as the delivery rate obtained will be higher than the slope of line I. Furthermore, any school should be taken when encountered if its combination of size and distance puts its delivery rate above the expected delivery rate from region B. Area A, despite being the richest, should not be harvested unless delivery rate drops to the slope of line II, point at which both places yield the same delivery rate to the home port. If the shape of the B' curve changes to B'_{low} due to decreased quality, then C becomes the best place, with schools $\geq S_c$ being sought, and area B should be dropped from the set of optimal fishing regions. At this point however, delivery rate from C is almost the same as in A, and practically any school size should be taken when encountered.

The Ensenada Anchovy Fishery

As was shown in Chapter II, the Ensenada anchovy reduction fishery usually begins in April, predominantly harvesting the coastal areas north of the port. As the season progresses, the central region -which is closer to Ensenada- is increasingly added to the exploited area. By the middle of the fishing season, harvest from the North area has diminished; the Central region is now being exploited more intensely; and there is some fishing in the areas South and Far South of Ensenada (see Chapter II for a description of the areas). In Figure 73 -constructed using Mexican fleet information for the period 1979 to 1985- it can be seen that during the fall there is a slight increase in the number of trips to the North region, but by the end of the

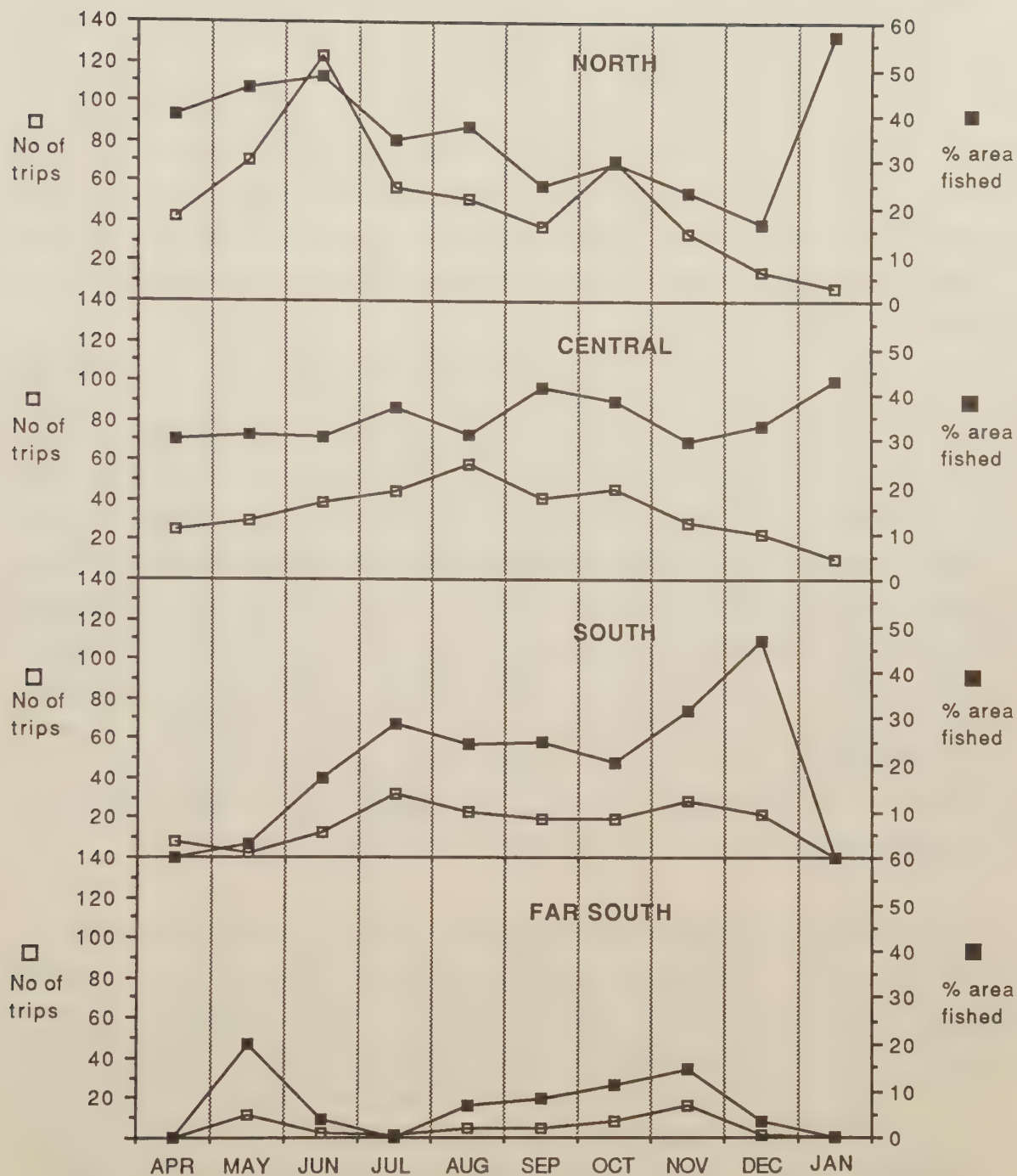


Figure 73. Monthly number of trips and proportion of area exploited, Ensenada fleet. The North area is fished heavily at the beginning of the fishing season. However, only the North area relationship is significant.

season all areas are being exploited at roughly the same rates, although the total number of trips has diminished considerably. However, the relative importance (proportion of total area exploited) of the northern area decreases throughout the season, while the significance of the Central area peaks in August; the contribution from the South region remains approximately constant and the proportion of area fished in the Far South peaks in November. There are apparently two peaks in the fishery: a large one during the summer months and a small increase coinciding with the fall season, perhaps when schools from the southern subpopulation become available in the South and far South fishing areas. However, only the trend in the North area is significant.

Catch per trip -average size of school captured or average size of load- increases with distance from port (as was shown in the section of optimal prey models), so that in general, the highest loads per hour per trip (e.g. delivery rate) are obtained in the South and Central regions throughout the year (see Figure 74, based on the same years of data as Figure 73). There is a peak during the summer in the Central region, and another late in the fishing season, in December. Delivery rate from the South region remains approximately constant, but peaks during the summer and again in December, coinciding with the highest delivery rate from the northern region, which is reached late in the fishing season as well. The northern coastal region receives a comparatively large number of trips considering that on the average it is more distant than the Central areas. Despite the large number of trips to this northern area, its distance from Ensenada explains why the delivery rate remains low throughout the year.

Assuming these trends are significant (apparently only the Central area relationship is), it is difficult to explain this particular fishing strategy under the Central Place Foraging model. Delivery rates are consistently higher from the central areas except in January when the North region becomes slightly better. However, if central areas are not considered, delivery rates are approximately equal for the remaining sites (particularly between August and November; at around 10 tons per hour per trip). This may indicate that -depending on whether the particular site is or not in the closer, central area- there are only two fishing regions of importance for the Ensenada fleet. That is, fishing places could be simply classified as those inside and those outside a central range.

Alternatively, the explanation of this fishing behavior may be found in the

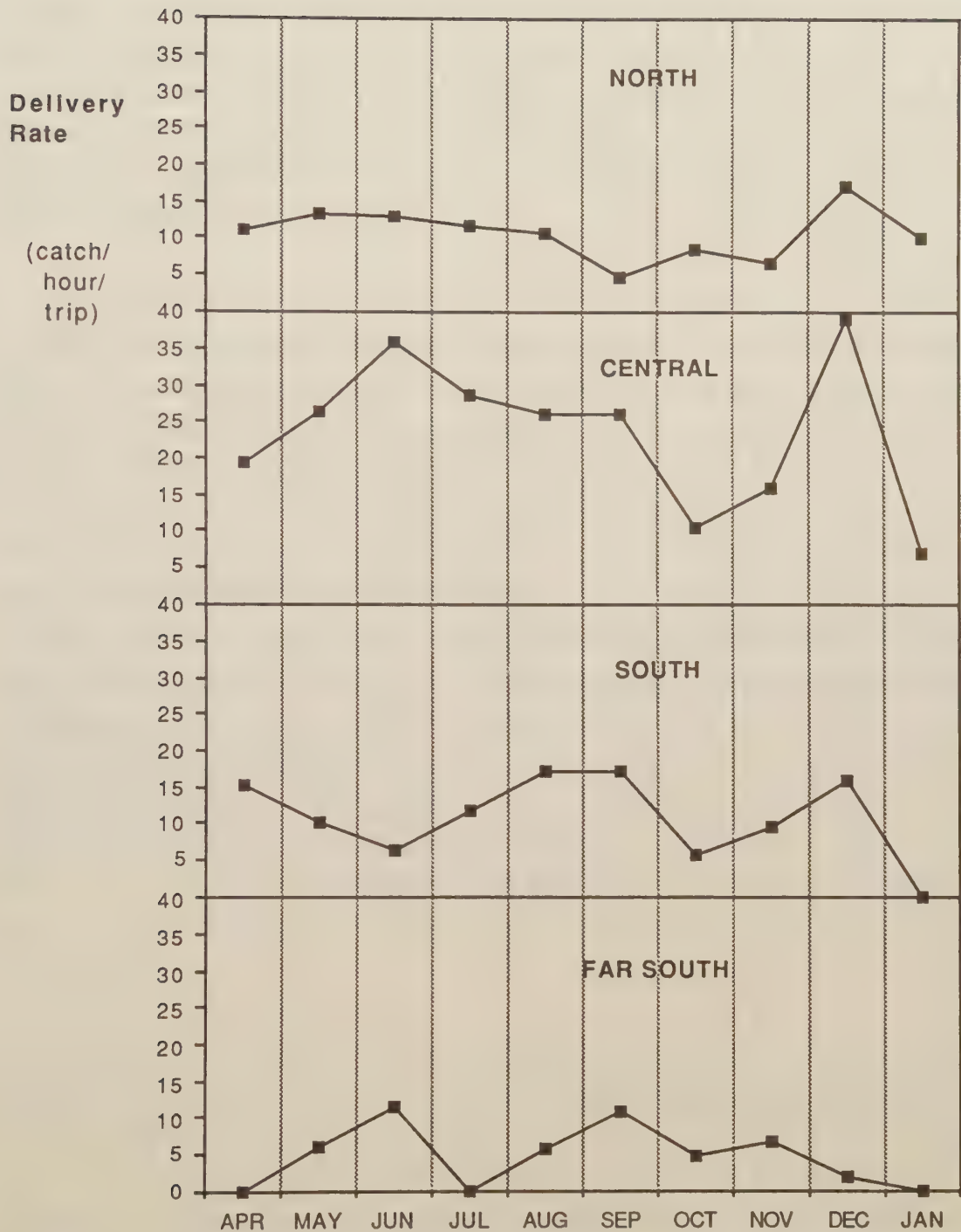


Figure 74. Monthly delivery rate, Mexican fleet. The central area has the higher delivery rate. North and Far South regions have comparable rates. There is an increase in fishing in November and December; but the only significant trend is in the Central area.

relative cost of traveling to each area. The Mexican government subsidizes fuel for fishing. This relatively low cost of fuel may make a trip to the northern area cost the same as a trip to the closer, central region. The assumption of equating time traveling with cost made in Figure 74 when estimating delivery rate would then be violated. Another possible violation of this assumption of cost as hour traveled may happen due to the effect of winds and currents. The combination of these two factors can conceivably make a loaded return trip from the northern area less expensive than a return trip from the closer central region.

Finally, the explanation to the apparently suboptimal behavior of harvesting so frequently the northern areas may also lie in the relative availability of schools in the different regions, particularly during the summer. It is possible that schools in the northern areas are more numerous but smaller than those found near Ensenada. If the difference in school size is large enough, the added cost of traveling more can be relatively unimportant (especially if fuel is relatively inexpensive). Another possibility is the artificial separation of areas. The regions considered here are the Zapata Company statistical areas, but they may not be reflecting any underlying patchy structure in school distribution. For example, North and Central large regions may be considered only one for fishermen, as the difference in average traveling time is small (especially to the most productive northern areas, El Descanso and Sal-sipuedes; see Chapter II). Finally, the possibility that the central place model for patch selection may not be adequate to describe the observed spatial fleet behavior of the Zapata Company should always be kept in mind.

IV FINAL CONSIDERATIONS

After reviewing the major aspects of Optimal Foraging Theory, and in particular Central Place Foraging, it is clear that these ecological models originally developed for natural systems have parallels and analogies in fishing systems as well. Fishing can be regarded as hunting, with the fisherman in a "superpredator" position. Thus, much of the theoretical basis of ecological models in foraging and predator-prey

systems can be applied to man (Millington, 1984) because fisherman are responding both functionally (e.g. fleet movement patterns) and numerically (e.g. harvest rates) to fish distribution.

The theory reviewed here is particularly important for the management of small pelagic fisheries systems such as those exploiting sardine and anchovy, but with appropriate modifications it can be applied to both large pelagic fisheries (e.g. tuna, whales) and groundfish fisheries.

The consideration of the northern anchovy fishery system as a problem in Central Place Foraging provides a convenient theoretical framework for the study of the heterogeneity patterns in the anchovy fishery reviewed in Chapter II. For example, these foraging models -and especially the single school Central Place Foraging solution- explain the concentration rings in fishing effort and harvest observed in both the U.S. and the Mexican fleets. The theoretical framework is also adequate to describe the monthly delivery rates and the average school size caught (e.g. catch per trip) in the Mexican fishery.

These considerations are particularly important because the Central Place Foraging theory is flexible enough to accommodate the particular characteristics and constraints of the northern anchovy fishery. Accordingly, the modification of the basic Central Place Model offers a solid theoretical basis for the description of the fishery and therefore it provides alternatives for management. For example, it was shown that varying the landing limits imposed by canneries and modifying the closed area would certainly make a difference to fishermen in terms of the school size sought and the delivery rates to the central port considered optimal or economically feasible.

The theory however, has critical -and restricting- assumptions. For example, the solutions developed consider that a fisherman travels to a certain place and then begins to search for an appropriate school. The decision as to whether to pursue or ignore the school encountered are then made at this point. A typical fisherman however, will constantly be searching for schools, and it is also likely that there will be simultaneous school encounters, violating the sequential school detection assumption of the theory.

Likewise, the decision as to which location to travel is seldom made blindly, because it is almost always influenced by experience, spotter airplane information

and communication with other fishermen. Therefore, the assumption of complete information is seldom fulfilled, but at least it is closer to be true than it is in most natural systems for which the theory was originally developed.

However, the set of rules that comprise the body of foraging theory -as was shown when describing the anchovy fishery- are flexible enough to accommodate changes due to constraints. For example, Stephens and Krebs (1986) have formulated modifications to the basic foraging models that can also be applied to fisheries. These changed constraints models could take into account the effects of sequential versus simultaneous encounters, the mutual exclusivity of search and handling, the selection of schools with sequential dependence, travel restrictions, the relative value of similarly sized schools (e.g. the problem of mixed species schools), sensory and detection limitations, risk-sensitive fishing and the incomplete information problem.

In summary, the 'Fishing as Foraging' approach, and in particular the Central Place treatment is extremely useful when describing space utilization patterns (i.e. concentration rings), and the factors that produce them. By making the appropriate assumptions and analogies, the theory provides a solid theoretical background that can be used to understand time and space heterogeneity in both the population and the fishery reviewed in Chapters I and II.

Therefore, Optimal Foraging Theory and in particular Central Place Foraging models can be very valuable for fisheries management, in particular for -but not restricted to- those systems in which fishing vessels have a home port to where they need to return after a limited amount of fishing time. The approach may be especially useful for several important management issues in various types of fishing systems, including small pelagic species (sardine and anchovy), large pelagic species (tuna and whales) and groundfish fisheries (flatfish). For example: the assessment of the cost of area closures and similar fishing regulations; the prediction of the amount of effort devoted at a certain time to a given area; and to determine the effects of limits on number of trips and in landings used frequently as regulatory measures.

CHAPTER IV SUMMARY AND DISCUSSION

I SUMMARY

The title of this work, "Spatial behavior of fish and fishermen : the use of habitat selection and optimal fisheries theory in fisheries", summarizes the unifying theme behind the dissertation. This basic idea is the interaction between population ecology theory and an applied ecological problem, fisheries systems.

The research supporting this dissertation thus combines two fields that have been seldom studied together -despite their conceptual similarity-, although both have been explored in detail separately. Direct interaction between fisheries and population ecology is achieved in two different ways:

First, the ecological theory of habitat selection is used to describe spatial distribution patterns of commercial fish populations. This is an ecological problem that has fisheries significance because it is relevant to the stock concept, a basic tenet of fisheries theory.

Second, optimal foraging theory (an ecological theory of resource utilization) is adapted to the fisheries context. This allows the consideration of the ecological problem of fishermen as predator. This is the translation of ecological theory into a fisheries framework, strategy that provides insight into fisheries management.

The rationale behind these ideas is straightforward enough: most theoretical models of population regulation consider the population as a collection of phenotypically identical individuals inhabiting spatially homogeneous habitats. In a similar way, most fisheries models deal with the concept of a fish stock, considered as a closed, self sustaining group of individuals forming a unit within which fishing mortality is proportional to fishing effort.

This fisheries assumption requires a uniform distribution of fish (e.g. complete mixing) and a random distribution of fishing effort over the fishing area. However, empirical data show that fish populations and fishing effort distributions are generally not uniform, both over space and time domains. This heterogeneity is clearly affecting some of the basic assumptions in fishery theory. Thus, the interaction between fisheries and ecological theory allows the direct examination of basic (and as yet unresolved or poorly studied) fishery problems in assessment and

management. As example of the types of problems that can be addressed using this approach are the question of definition of a unit stock -spatial behavior of fish- (Gauldie 1985, Sharp 1983) and seldom considered aspects of spatial behavior of fishermen and fishing fleet dynamics (Hillborn, 1985a).

This dissertation is therefore concerned with these homogeneity assumptions, in particular with the complete mixing and the uniform distribution of fish populations it is supposed to produce; and with the randomness of fishing effort and independence of fishing units. This work is also concerned with some consequences of the violation of these assumptions, especially as they relate to the spatial behavior of fishermen (e.g. similarities between foraging theory and fisheries).

The main objective of this study is thus to address the problem of interaction between a spatially fluid and structured fish population (e.g. the effects of expansion and contraction, clinal variation and incomplete mixing); and a fishery with limited spatial range (e.g. the consequences of a fishing fleet viewed as a local perturbation). This approach allows to investigate some basic fishery questions derived from the above line of thinking :

- In what ways and to what extent does a fish population display structure and spatial flexibility ?
- What kind of patterns are typical of a "local" fishery ?
- What are the implications of these problems for fisheries assessment and management ?

In exploring answers to these questions, this work describes examples of heterogeneous fish distributions using several clupeoid based fisheries systems, in particular the one relying upon the northern anchovy (*Engraulis mordax*). This fishing system also serves to describe heterogeneity in the distribution of fishing effort employing information from both Mexican and U.S. fishing fleets. In addition, and based on fish and fleet spatial behavior, management models are developed by adapting ecological ideas on optimal and central place foraging theory to the performance of the northern anchovy fishing fleet. Some implications of these theoretical models are also explored.

The problems of fish population heterogeneity in clupeoid populations are reviewed in Chapter I. Variation in spatial distribution -range expansion and contraction-, as it relates to changes in abundance over large geographical areas (e.g. population spatial flexibility) is described. The issue of non uniform individuals is studied using the ecotypic or clinal variation in age composition and growth rates (e.g. population spatial structure).

The theoretical framework for the study of both fish population flexibility and population structure issues is provided by the theory of Density Dependent Habitat Selection, and in particular by the notion of the Ideal Free Distribution. These ideas and the models developed can be used to conveniently describe patterns of spatial change, in the form of expansion and contraction of feeding and spawning ranges with changes in population abundance.

Many clupeoid species exhibit these abundance related changes in space utilization, and examples from egg, larva and adult distributions are examined for several commercially important fish populations: the northern anchovy, the Pacific sardine and the Peruvian anchoveta. The study of clinal patterns (variation along a geographical gradient) in growth and mortality in the northern anchovy, shows that mixing within the population may be limited, phenomenon that has important implications for fisheries management because of its implications of a non uniform distribution of individuals.

Results from this chapter clearly show that in general, clupeoid populations can not be considered spatially homogeneous. Also, it is proposed that fishing can be a directional force that selects against those individuals that form the spawning peak and live mostly at the center of the distribution (presumably 'strong', highly adapted fish). The recovery of such a population after fishing is then highly dependent upon the 'weak', peripheral individuals, that is, the part of the population that spawns before or after the spawning peak.

Heterogeneity in the fishery is examined by reviewing spatio-temporal patterns in aerial effort, sightings and harvest distributions in Chapter II. The results of the analysis show that both Mexican and U.S. fleets exhibit a highly heterogeneous spatial behavior: the U.S. fleet usually operates in the San Pedro Channel, where the effort is most of the time aggregated, particularly during the spring and fall fishing seasons; the Mexican fleet exploits a somewhat larger area, but the vessels are also

confined to a very narrow coastal region. Both fishing fleets however, exhibit similar patterns when concentration rings (e.g. boat distribution around the home port) of harvest and fishing effort are considered. These distance-decay relationships are probably similar for the two fishing fleets because they respond to constraints inherent in the anchovy resource and the fishery system.

Some aspects of behavior of fishermen are conveniently summarized by the mean and the variance of the distance (measured from the home port) at which the actual fishing set takes place. The results show that the average distance a fisherman is willing to travel is not directly related to anchovy abundance for low density levels. It seems that harvest takes place mostly from the center of the population distribution during years of high anchovy abundance and predominantly from the periphery when density is low. If this is true and the population does not mix completely, as findings in Chapter I suggest, then fishing has a differential impact on the anchovy population, affecting mostly old individuals some years and predominantly young animals in others. This particular result has clear implications for fisheries management and assessment.

Mean distance of sightings and fishing, in conjunction with several economic and biological variables are also used in a factor analysis. Five significant components are extracted; the most important being different measures of fishing effort; mean distance of harvest and sightings; and economic variables. Factor scores and the empirical analysis performed show that, not only biological but also economic forces are very important to the analysis of the spatial heterogeneity (e.g. behavior of fishermen as indicated by vessel distribution) in the fishery.

The theoretical framework for understanding these fishery patterns -in particular fleet movements and concentration rings- is provided by the ecological theory of Optimal Foraging (OF) and its particular case, the Central Place Foraging idea (CPF) reviewed and modified in Chapter III. The basic underlying assumptions in this chapter are that fishermen can be considered a predator and that anchovy schools can be treated as their prey. Thus, fishermen respond both functionally (space and time fleet movements) and numerically (harvest rates) to changes in anchovy abundance.

Optimal prey and optimal patch selection models that comprise the body of Central Place and Optimal Foraging Theories are modified to examine characteristics particular to the anchovy fishery system. Thus, the models are adapted to study

the problems of optimal selection of school types (school size discrimination) and of distribution of fishing areas as a function of their distance from the fishing port.

Data from both Mexican and U.S. fleets are also employed to empirically describe the northern anchovy fishery using the optimal foraging approach and to test some predictions of the theory. The results show that delivery rate of individual boats decreases with increased distance of the fishing site from the home port. However, the mean school size captured increases with distance from port. Both patterns agree with predictions from Central Place Foraging theory, and explain the observed concentration rings. The single school loading model of CPF is modified and adapted to include characteristics specific to the northern anchovy fishery, such as a reduced coastal area for operation, landing limits for vessels, small vessel size and the use of airplanes to search for fish schools. The resulting models show that the theory can have a useful application in fisheries management, particularly for the assessment of effects of area closure and for the forecast of the amount of effort that will be applied in a particular region at a given time.

II DISCUSSION

The dissertation progressed from the empirical description of basic heterogeneity in fish populations, both in space and time, through the experimental description of the behavior of fishermen as reflected by fleet movement patterns, to the theoretical study of fishermen and fish under the ecological framework of optimal foraging theory.

Two elements point out to the fact that fish populations can not be considered homogeneous :

The first is the expansion and contraction of spawning and feeding range observed in clupeoid populations. This phenomenon introduces important changes when considering sampling and assessment of fish populations, and -among some other issues- when using catch per unit of effort as a measure of abundance. In this context, spatial behavior of fish is adequately described by the ecological theory of density dependent habitat selection, and its associated ideal free distribution. The basic idea is that individuals do not feed or reproduce in marginal areas (e.g.

peripheral regions where ecological conditions are not optimal for the population), until the quality of central areas decreases due to the effects of increased population density.

The second is the variation of biological characteristics along environmental gradients (e.g. clinal change) in growth and age composition. Distinct geographic areas have been identified for clupeoid populations, with different schedules of growth and mortality. The existence of these clinal variations indicates that individual movement is not sufficient to spread out the effects of the environment and other factors (e.g. fishing) to the whole population. The net result of this lack of internal mixing is a well defined spatial heterogeneity.

The combination of these two factors has important implications for fisheries management: When considering these types of populations, the concept of biological viscosity (e.g. the ability of the population to spatially 'flow' or mix, which allows to assimilate changes) should be taken into account, and the issues of local populations, meta populations (very large, open populations with local recruitment) and local rates of recruitment, growth and mortality should be examined in detail.

The consideration of a stock composed of relatively isolated local units, each one with a distinct schedule of growth and mortality along physical environment gradients, and responding to fishing pressure and variation in the environment by expanding and contracting occupied areas, certainly departs from the traditional concept of a stock as a relatively closed, homogeneous, self sustaining group of fish (Gulland 1983, Sharp 1983, Gauldie 1985) and requires the development of new techniques and conceptual models for the adequate assessment and management of fisheries.

However, in order to obtain a complete picture of heterogeneity in a fishery system, the effects of variation in the behavior of fishermen should also be considered. Fishermen respond dynamically to variations in resource abundance and distribution, and to changes in the economic forces by modifying their fishing strategy. One way to study this variation in clupeoid fisheries is by looking at patterns of fleet/aircraft movement.

As was the case with the distribution of fish, both empirical and theoretical studies of fishermen behavior point out to the fact that the fishery (e.g. spatial and temporal distribution of boats and fishing effort) can not be considered homogene-

ous.

The nature of concentration rings of fishing effort and school sightings around the fishing ports, indicates that fishing mortality should be considered a local but very significant dynamic force acting upon clupeoid populations. For example, the spatial domain of the boats is small when compared to the distribution range of the anchovy population, but the fishing fleet usually operates at the center of the fish distribution, and thus have a relatively high impact on mortality.

The approach of considering fishing mortality as a distance decay phenomenon is very different from the usual perspective of viewing the effects of fishing effort as uniformly distributed (either by vessel movement, fish distribution changes, or a combination of both). This new approach requires the development of new methods and it affects measures such as CPUE as an index of abundance; as well as the recruitment problem and the estimation of fishing and natural mortality by traditional approaches.

In addition, the use of foraging theory allows the inclusion of this variation and spatial heterogeneity into fisheries management and assessment techniques, because it provides a convenient theoretical framework for the analysis of fleet movements and for the study of fishing effort distribution in the dynamics of fish populations. This ecological theory is also apt to be modified to explore some consequences of new management options that consider explicitly patterns in spatial variation of fleet movement as a consequence of changes in resource abundance and distribution.

FISH AND FISHERIES HETEROGENEITY

What are the consequences of these heterogeneity factors for fisheries management ?. How does the relationship between the incomplete mixing problem and the consideration of fishing as a local disturbance with varying spatial and temporal scales affect fisheries techniques ?.

The answer to these basic questions depends on the degree of heterogeneity displayed by fish and fishermen. Solutions are different for distinct conditions in the variation spectrum, ranging from the point where both fish population and fishing fleet distribution are homogeneous to the scenario where both fish population and fishing fleet distribution are heterogeneous.

If fish are homogeneously distributed and internal mixing is high due to active individual movement, then the fish population approximates the theoretical assumptions of most traditional fisheries models. Likewise, if fishing effort is uniformly distributed in space, -and if the previous assumption of fish distribution homogeneity holds- then the basic tenets of fishery management based on historical fisheries models can be considered true. For example, under these ideal conditions, CPUE will be a perfect index of abundance because fishing effort will be proportional (and this proportionality will not change) to fishing mortality. Thus most of the traditional sampling and management fisheries techniques developed for these theoretical populations will work satisfactorily. This is no trivial conclusion, as the large body of literature testifies, because under certain circumstances both fish and fishermen's behavior can be viewed as producing a spatially uniform, homogeneous fishery system. However, as this study demonstrates, it is usually very difficult to assume with a degree of certainty that the homogeneity conditions are met.

The first heterogeneity scenario to consider occurs if the fish population spatial distribution is heterogeneous but the fishing effort deployed can be considered homogeneous. In this case there are at least two aspects of the problem that should be addressed :

The first is a density dependent phenomenon, namely the expansion and contraction of feeding and spawning areas. This problem can be examined using ecological theory of density dependent habitat selection and the ideal free distribution. Some fisheries management implications of this fish behavior can be worked out by allowing the coefficient of capturability that relates fishing effort and fishing mortality to vary with changes in abundance (e.g. MacCall, 1976); and by considering the extent of the area inhabited by the population as an indicator of its overall state (e.g. Sharp, 1981). Both approaches offer modifications and alternatives to traditional fisheries models used for management, but require extensive sampling and detailed analysis, and these limits severely their applicability. However, useful information on spatial behavior could be obtained from catch and effort data, supplemented with resource assessment sampling.

The second aspect of the fish population heterogeneity problem introduces a potentially more difficult issue : the clinal variation of growth and mortality schedules can be considered largely a non density dependent problem, but it has implications that may affect both the expansion and contraction phenomenon as

well as the application of fisheries management models. The clinal variation in fish populations can be described by the usual sampling of age and size data (e.g. Parrish *et al* 1985) and by genetic approaches to stock separation, but detailed evaluation of mixing rates among 'local populations' or 'subgroups' within the population -each with its own growth and mortality schedule- , would require extensive mark and recapture studies. At issue here is the biological diffusion problem : to what extent a population can be considered as composed of relatively independent subunits, differing in physiological status ? (e.g. The elementary populations concept proposed in 1969 by Levedeb). This dissertation shows that it is necessary to have detailed information for high and low biomass periods just to identify the phenomenon. The problem is additionally compounded by the effects of changes in the fishery and the consequent variation in fishery data availability they produce (e.g. Mathisen 1979).

Despite these difficulties, a modeling approach can be useful here, combining for example the concept of as fish population as composed of different subunits with varying mixing rates but allowing each subunit to spatially expand and contract with changes in abundance. In this way way, the coefficient of capturability " q " will vary within each subunit, depending not only on the age and size composition of individuals but also according to their abundance. The area occupied by each subunit would indicate the overall dynamics within its boundaries, but the expansion and contraction of a population would depend on the relationship of all these factors with mixing rates; as well as on the effects of environmental variation which would affect age and size composition within each subunit.

The effect of fishing introduces another level of complexity to this problem. If fish distribution has some degree of homogeneity, then fishing effort can be conveniently described by using concentration rings and distance decay functions. These empirical models can be incorporated into fisheries management options that allow special variation in fishing rates. Thus, in the modeling example described above, fishing would be introduced in the system as a local disturbance, affecting the growth and mortality schedules of those population subunits close to the fishing port, but its overall impact on the population would depend again on mixing rates.

As shown in this work, one convenient way to introduce spatial variation in fleet behavior is by using optimal foraging and in particular central place foraging theories which provide a powerful theoretical framework for the study of fleet

movement. If the basic assumption of considering fishermen as natural predators holds, both theories are useful as first approximations for modeling fisheries and for the considerations of specific constraints to a given system, as was shown in chapter III. This fishermen's behavior models will become more useful when coupled with heterogeneity models of the kind described above. However, under certain conditions they could be used as stand-alone tools for management, as the northern anchovy fishery case demonstrates.

The second, more complex scenario arises when both fish and fishing distributions are heterogeneous. In this case the explicit consideration of biological diffusion rates, mixing and the encompassing concept of biological viscosity or flexibility become important. Under these circumstances, the idea of fishing as a regional disturbance of local impact becomes of importance as well. However as it was the case with the first scenario, the overall interaction between fish and fishing heterogeneity depends upon the degree of mixing the population or the different population subunits display.

If mixing rates are low (e.g. biological viscosity is high), the effects of fishing and the environment are not spread out to the entire population fast enough. Then, fisheries can be considered equivalent to various ecological phenomena (e.g. forest fires and disease) that produce local system disturbance and consequent depletion and replenishment patterns. Under this situation, fishing effects upon only a portion of the population are of prime importance. The fishery has a more or less spatially constant impact area over an ever changing anchovy population (e.g. the stern stele model in Figure 1 of Introduction), and the disturbance is usually higher near the center of the distribution or at least near the center of higher density. In this case, the application of management models based on the homogeneity of fish and fisheries assumption, must be made with extreme caution; and the estimation of fishing mortality and optimal yields for the entire population should take into account all these characteristics.

On the other hand, if internal mixing rates are high (e.g. low biological viscosity), then the effects of fishing will probably be spread out over the entire population. In this case, most standard fisheries techniques for assessment and management can be applied. However, it should be taken into account that spatial phenomena such

as the expansion and contraction patterns and the highly seasonal nature of concentration rings around the fishing ports are of extreme importance.

The large impact of these population heterogeneity and internal mixing problems in fisheries management and assessment, underscores some basic limitations of most traditional fisheries models.

One is the lack of consideration that understanding the relationships between catch per effort and fish abundance requires looking at both the fish and the fishermen (Hillborn 1985a). As this study has shown, the interplay between the spatial distribution of fish and the spatial distribution of effort should be of utmost importance for fisheries managers and researchers.

The other is the lack of direct consideration of space in population dynamics (see discussion of this topic in Taylor and Taylor, 1977). Despite the basic biological fact that an individual rarely grows and reproduces in the same place as its parents, spatial distribution has been considered more a statistical nuisance than a legitimate component of population dynamics (Margalef, 1986). Extending to fisheries the idea of Taylor and Taylor (1977), it can be stated that only looking at fish populations and fleet distribution as changing over both space and time will allow us to consider a truly dynamic view of the fishery system.

III PERSPECTIVES

THE ECOLOGICAL APPROACH

Using ecological theory to describe fisheries is an approach seldom employed that opens further possibilities for understanding fisheries systems and offers alternatives for fisheries management.

For example, the relation between optimal foraging, habitat selection, fisheries exploitation and management can throw light into both fisheries management and ecological theory. Some alternatives for the interpretation of catch per unit effort under foraging theory have been suggested in this work. In general, fishing mortality could be spatially adjusted by the use of distance decay functions and

empirical information on concentration rings.

Alternatively, the anchovy fishery example can be used to expand optimal foraging theory. Examples of this approach are the "last change" strategy proposed in Chapter II and the problem of the amount of information on prey abundance and distribution the predator needs to make adequate foraging decisions. The system studied in this work included two predators (U.S. and Mexican fleet) with varying degrees of information. The use of airplanes by the U.S. fishery allows Southern California fishermen to obtain a clear picture (in almost real time) of fish abundance, as demonstrated by seasonal variation in spatial distribution of effort. On the other hand, the Mexican fleet seldom uses scouting airplanes, but the information exchange among fishermen increases as the fishing season proceeds because most of the fleet belongs to only one company. A direct comparison between these two predator's information gathering strategies was not attempted in this work, but it could be carried out with adequate data.

Despite its potential usefulness, the foraging approach has limitations that complicate its application to populations. It deals with the behavior of individual predators, but the consequences of this individual behavior for population dynamics have just begun to be theoretically explored. However, this limitation is perhaps not as important in fisheries management, where the notion of fleet behavior or spatial distribution is not strongly considered (in most instances fishermen are treated more or less individually). If this "individual to population" problem is solved, optimal foraging theory can be used in fisheries with a minimum of assumptions. For example, when estimating fishing power, optimal foraging could be used to adjust for different vessel searching, handling and roundtrip capacity. Also, the expansion of the OFT analogy to fleet behavior (e.g. 'population' of individual fishermen) could be carried out to encompass not just the population, but the whole 'ecosystem'. In this case this would include the economic, social and market forces regulating fishermen behavior and therefore fleet distribution.

It should be pointed out that the ecology-based approach used in this dissertation is far from being a solution for fisheries management and assessment in clupeoid fisheries. However, this ecological view of fishery problems can provide a good basis for an increased, mutually beneficial exchange between both Ecology

and Fisheries Science.

This analogy between fisheries and ecological systems can be further extended to other fields. A brief description of specific areas follows.

- The ecological theory of disturbance and ecosystems (e.g. Mooney and Godron, 1983) has been developed mainly to describe patterns when plant communities are subject to perturbations such as fire, diseases and flooding. This theory can be applied to fisheries; in particular when mixing is low (the high viscosity situation). In this ecological context, problems such as the selective removal or harvest of desirable species become very important. The basic idea is that fishing can be considered a man-made disturbance in the ecosystem, and as such, is no different in its effects from a plague, a killing fire or a sudden flooding. Furthermore, fishing is usually a perturbation of known intensity, generally regular in time and space, and to certain extent it can also be predictable.

Several levels of response in such a system can be distinguished: for example, among the disturbance characteristics that have relevance to fish response we can include the size, intensity, frequency, regularity, and duration of the fishing event. Among the population characteristics responsive to disturbance are density and dispersion, growth rate, survivorship, age and size structure, and competitive interactions. Thus, some fish life history characteristics that may be affected by disturbance are spatial and temporal dispersability and reproductive strategies, such as breeding, fecundity and reproductive allocation. At the community level (Pickett and White 1985) diversity, trophic structure, competitive interactions and succession (which may be very important if mixing is very slow) are all affected by the nature of the perturbation. Finally, whole ecosystems may be changed if energetics and nutrient cycles are affected by the fishing perturbation.

Fisheries theory will benefit from this ecological analysis of fishing, and from all the studies already done on patch dynamics and succession. Likewise, ecological theory will benefit from the large empirical data base on frequency, magnitude and effects of the fishing disturbance. This effort may contribute significantly to the development of a formal disturbance/fisheries theory capable of generating testable hypothesis in a wide range of marine ecosystems.

Furthermore, the consideration of fisheries as an ecological perturbation allows the inclusion of phenomena such as resource depression (Charnov *et al* 1976) into fisheries thinking. It is also worth noting that this type of reasoning is leading

fisheries science towards a new threshold, namely the rethinking of fisheries research to follow an “ecosystems approach” in fisheries management and assessment (for examples see recent work by MacCall 1986, and Caddy and Sharp 1986).

- Social studies of fisheries and fishing have made analogies between the ecological life cycle of an organism and the exploitation phases in an ideal fishery system (Smith 1986). Under this proposition, the life history of a fishery becomes a progression of uses which begins with commercial, then adds recreational, and finally aesthetical values. According to the author, this flow of events is driven by the increased number of people using the fish stock and by economic activities that reduce the stock habitat.

Although such a fishery system is highly simplified, the idea of considering a fishery as a dynamic, changing ‘superorganism’ is new, and its potential usefulness in fisheries management is high. For example, fisheries management interferes with the ‘normal’ life cycle of the fishery because, -being usually a mere choice between conservation and allocation-, it attempts to slow or stop the process of change. In our growing society, (if management objectives are not achieved), the fisheries life cycle process will continue to be driven only by the increased number of users.

This approach can benefit not only by the consideration of a fisheries system as an organism, but -carrying out the analogy one step further- also with the incorporation of the dynamics of organisms under evolutionary pressure; that is, the explicit consideration of life history patterns and strategy would become relevant. For example, the ‘reproductive patterns’ of different users and their relative ‘fecundity’ and ‘reproductive allocation’ would shed light into the changes the fishing system experiences during the different life cycle stages. These analogies are useful because they allow to consider the evolution of the life cycle of a fishery as driven not only by the increase in number of users; but also as affected by changes in their growth rate (e.g. different users in varying numbers) and its impact on the whole fishing system.

- Some alternatives to the solution of the problem of shared stocks and transboundary species can perhaps be found in ecological models of predator-prey systems and competition. Although this approach is not new (e.g. Beverton and Gulland 1958) there are now new research directions and added pressure to find satisfactory alternatives.

For example, Caddy (1982) discussed definitions of shared stocks and the problems associated with resource allocation between countries and/or fishing fleets. As was pointed out when reviewing OFT and CPF in Chapter III, Caddy's approach could be enhanced using the analogy of fishermen as predators competing for resources. In this way, commercial versus recreational uses (or any other conflicting single use activity) can be looked at as predators displaying different resource use strategies.

The fleets of different countries can also be viewed in terms of generalized versus specialized predator's strategy. Such is the case of the northern anchovy fishery where the Southern California fleet is able (with only minor modifications) to switch to a different prey if market or biological conditions warrant it. On the other hand, the Mexican fleet is geared toward capturing anchovy and it would be very difficult to adapt the boats for the harvesting of other species. Thus, due to technical, social and market constraints, the U.S. fleet is opportunistic in its approach to anchovy fishing, while the Mexican fleet is highly specialized.

Benefits for shared stocks for competing fleets can probably be derived using already developed ecological models for competing predators. For example, McKelvey (1983) and Smith and McKelvey (1986) in their study of fishermen's behavior use the terms specialist and generalist to describe a strategy to cope with resource variability. Specialists typically operate and invest in only one fishery and therefore, their cost of changing to a new fishery is very high. This type of fisherman looks more to the long term benefit and average their economic return over time, preferring stability and consistency. Generalists (or opportunistic) by contrast, participate in many activities. They seek to minimize the cost of switching between activities by fishing in multipurpose vessels. Their perspective is short term, thus stability and consistency do not have the same relevance for them, and they average over opportunities rather than over time.

This dicotomy is very similar -at least in spirit- to the familiar ecological theory of r and K selection (Pianka 1970, and a fisheries application by Caddy 1984). According to this theory, r species are selected to favor productivity and are therefore opportunistic, with rapid development and large reproductive output. The K species on the other hand, are selected to favor efficiency and thus they are specialists, with slow development and low reproductive output. These characteristics are in agreement with Smith and McKelvey (1986) generalists versus special-

ists categories. The large body of literature on this ecological topic (r-K selection and life history strategies) can be very valuable for the development of a similar, but empirically based theory on the behavior of fishermen (see for example Bockstael and Opaluch 1983).

This approach is not unlike that proposed by Clark (1985) in bioeconomic modeling of search and capture strategies. The author develops the notion of concentration profiles, which are a formal version of the empirical concentration rings examined in this dissertation. The approach allows to study both diffusive and aggregative resource stocks along with some management implications. Results similar to those central place foraging predicts are found using Clark's bioeconomic decision models that include passive and active fishing strategies and their role in fishermen's behavior and fisheries management decisions. Clark also consider the main complication added by multispecies fisheries and the effects of stock abundance fluctuations and uncertainty.

These are all fisheries problems with close analogies in ecology and economics, but in most cases they could be easily adapted from their original areas to the field of fisheries research. Since the solutions to some of the ecological alternatives are already known, there are added advantages and benefits for both fisheries and non fisheries approaches.

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